The first skeletal evidence of a dicynodont from the lower Elliot Formation of South Africa

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Historical fossil specimens from the lower Elliot Formation are identified as representing a large-bodied dicynodont, the first known from skeletal material in the Late Triassic of South Africa. Although fragmentary, these fossils differ from all other known Triassic dicynodonts and are here described as a new taxon, *Pentasaurus goggai* gen. et sp. nov. *Pentasaurus* can be distinguished from other Triassic dicynodonts by a number of mandibular characters, most importantly the well-developed, unusually anteriorly-positioned lateral dentary shelf. Phylogenetic analysis indicates that *Pentasaurus* is a placeriine stahleckeriid. Placeriines include the latest-surviving dicynodonts but their remains are primarily known from the Northern Hemisphere, with their only previously-known Southern Hemisphere representative being the Middle Triassic Zambian taxon *Zambiasaurus*. The discovery of a placeriine in the Late Triassic of South Africa supports recent proposals that local climatic conditions, not broad-scale biogeographic patterns, best explain the observed distribution of Triassic tetrapods. The tetrapod fauna of the lower Elliot Formation is highly unusual among Triassic assemblages in combining 'relictual' taxa like dicynodonts and gomphodont cynodonts with abundant, diverse sauropodomorph dinosaurs.

Keywords: Synapsida, Therapsida, Dicynodontia, Triassic, Karoo Basin, biogeography.

INTRODUCTION

The Naturhistorisches Museum Wien houses a small but historically important collection of vertebrate fossils from the Karoo Supergroup of South Africa. The vast majority of these specimens were collected by the famous fossil hunter Alfred Brown, a reclusive and eccentric Englishman who spent most of his life in Aliwal North, Eastern Cape Province. Brown was one of the first collectors to find tetrapod fossils in the Late Triassic–Early Jurassic Stormberg Group; previous Karoo tetrapod fossils had mostly been found in the stratigraphically lower (mid-Permian–Middle Triassic) Beaufort Group (e.g. Bain 1845; Owen 1859). Brown's earliest fossil discoveries were made in the 1860s, and in 1866 he shipped a crate containing 350 fossil specimens to the noted geologist Sir Roderick Impey Murchison in London. The contents of this crate were immediately recognized by Thomas Huxley as containing the first definitive dinosaur remains from South Africa, including 'the thigh-bones of a great Dinosaurian reptile as big as Megalosaurus [*sic*] and probably nearly allied to it' (Drennan 1938, p. 37), which were soon described as *Euskelesaurus brownii* (Huxley 1866; note that although another South African dinosaur, *Massospondylus carinatus*, had been described earlier [Owen 1854], Owen did not recognize that taxon as dinosaurian, instead classifying it as a lacertilian). Brown promised to send additional crates of material following the recognition of *Euskelesaurus*, but because of late replies and general disinterest on Murchison's part, Brown soured on the deal and the London palaeontological establishment in general. Subsequent interactions with Parisian researchers left him similarly cold and increasingly skeptical of collaboration with European scientists, but he later accepted an offer from Nathaniel Adler, Consul for the Austrian Empire in Port Elizabeth, to send fossil shipments to the K.k. Naturhistorisches Hofmuseum (Imperial Museum of Natural History) in exchange for recognition as a Fellow of the Imperial and Royal Geographical Society of Vienna (Drennan 1938).

The Brown collections in Vienna consist of two major lots, accessioned in 1876 and 1886. The 1886 lot is composed primarily of fossils from the Middle Triassic Burgersdorp Formation (mostly specimens of the kannemeyeriiform dicynodont *Kannemeyeria simocephalus*, including the holotype skull of that species; Fig. 1D) and the Early Jurassic upper Elliot Formation (mostly specimens of small sauropodomorph dinosaurs; Fig. 1C). The 1876 lot is more intriguing, as it seems to be made up almost entirely of specimens from the Late Triassic lower Elliot Formation. Galton & Van Heerden (1998) reviewed the complicated history of Brown's early finds in the lower Elliot and their subsequent diaspora into European

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Figure 1. Representative vertebrate fossils from the Brown Collection at the Naturhistorisches Museum Wien, showing differences in preservation style between formations. Dinosaur fossils from the upper Elliot Formation (Lower Jurassic): NHMW 1886-XV-38, distal half of the left femur of an indeterminate dinosaur in (**A**) posterior and (**B**) distal views; NHMW 1886-XV-22, right humerus of a basal sauropodomorph in (**C**) anterior view. Dicynodont fossil from the Burgersdorp Formation (Middle Triassic): NHMW 1886-XV-4, holotype skull of *Kannemeyeria simocephalus* in (**D**) dorsal view. Dinosaur fossils from the lower Elliot Formation (Upper Triassic): NHMW 1886-XV-39, proximal portion of a left femur, part of the holotype of '*Aliwalia rex*' (=*Eucnemesaurus fortis*) in (**E**) anterior, (**F**) medial, and (**G**) posterior views; NHMW 1876-VII-B-124, distal portion of '*Aliwalia rex*' femur in (**H**) anterior, (**I**) posterior, and (**J**) distal views. Note distinctive brownish-grey colouration of the '*Aliwalia*' fossils compared to the reddish bones typical of the Burgersdorp and upper Elliot formations. Different views of single specimens to scale with one another. Scale bars equal 5 cm.

collections. They concluded that the London, Paris, and Vienna shipments were, per Brown's own testimony (Broom 1911), all collected at the same locality. Seeley (1894) identified this locality as Barnard's Spruit (a stream to the south of Aliwal North), and although alternatives have been proposed (Haughton 1924), current scholarship supports Barnard's Spruit as the type locality for '*Euskelesaurus brownii*' and associated material (Yates 2007).

Much to Brown's chagrin, nearly nothing was done with his fossils by researchers in Vienna, other than the description by Weithofer (1888) of the skull of *Dicynodon* (=*Kannemeyeria*) *simocephalus*. Huene (1906) later described a massive partial femur (broken into proximal [NHMW 1886-XV-39] and distal [NHMW 1876-VII-B-124] portions) from this collection as a specimen of *Euskelosaurus* (?) sp. [*sic*]. Galton (1985) reexamined this specimen (Fig. 1E–J) and made it the holotype of a new taxon of enormous herrerasaurian dinosaur, *Aliwalia rex*. Referral of *Aliwalia* to the predatory clade Herrerasauria was based on its possession of a well-defined and medially-directed femoral head with a constricted neck, prominent lesser trochanter lacking a dorsal process, and a large, protruding, proximally-positioned fourth trochanter. Seemingly corroborating this identification was a large maxilla bearing serrated, blade-like teeth (NHMUK R3301) among the material from Barnard's Spruit (Seeley 1894), which Galton (1985) referred to *A. rex*. Paul (1988) estimated that *Aliwalia* would have weighed ~1.5 tons, making it easily the largest dinosaurian carnivore of the Triassic and rivalling later Mesozoic taxa such as *Allosaurus* in size. Unfortunately for fans of giant theropods, however, Yates (2007) recognized that the type femur of *A. rex* actually represents a basal sauropodomorph ('prosauropod'), and furthermore could be referred to the long-ignored lower Elliot taxon *Eucnemesaurus fortis* van Hoepen, 1920. As part of this revision, Yates (2007) removed the referred maxilla from the hypodigm of '*Aliwalia*', recognizing it only as belonging to an indeterminate predatory archosaur.

In addition to the '*Aliwalia rex*' holotype, almost all of the other elements in the 1876 lot can be identified as lower Elliot fossils probably collected along Barnard's Spruit. These elements all show a similar style of preservation, concordant with that of '*Aliwalia*' in that they are fragmentary, weathered, and consist of brownish-grey bone in a fine-grained brown sandstone. Among these elements are three jaw fragments (NHMW 1876-VII-B-111, 112, and 113; Fig. 2) preserving the roots of large teeth comparable in proportions to those of NHMUK R3301. Although too fragmentary for definite identification, given their size they likely represent a 'rauisuchian' (a group previously considered present in the lower Elliot Formation based on dental [Kitching & Raath 1984] and footprint [Olsen & Galton 1984] records). The preservation of these elements

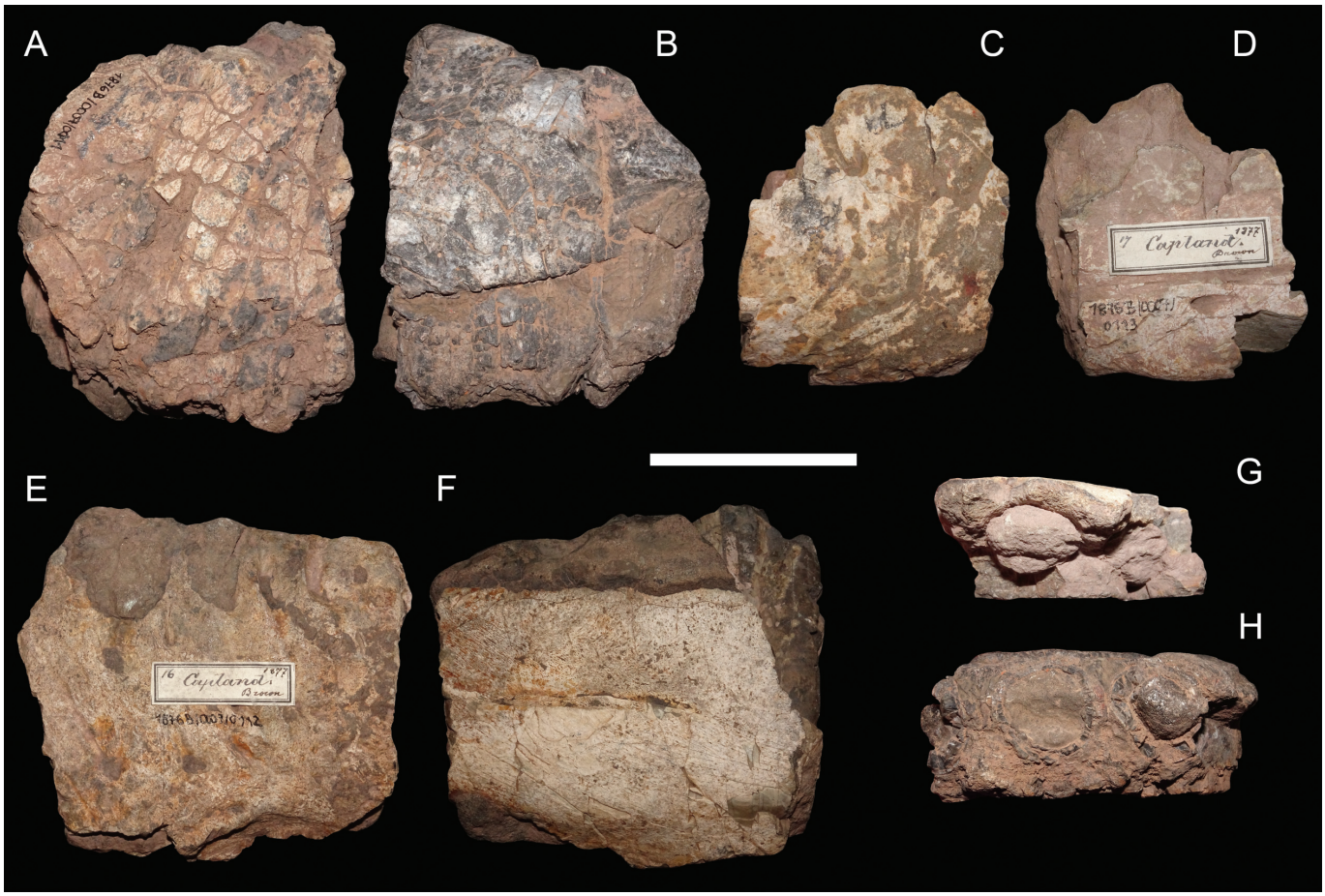

Figure 2. Jaw fragments of a large predatory reptile from the lower Elliot Formation, possibly the enigmatic lower Elliot 'rauisuchian' *Basutodon ferox*. NHMW 1876-VII-B-111, fragment of a left maxilla in (**A**) lateral, (**B**) medial, and (**H**) ventral views. NHMW 1876-VII-B-113, fragment of a right jaw symphysis in (**C**) lateral, (**D**) medial, and (**G**) dorsal views. NHMW 1876-VII-B-112, fragment of left dentary in (**E**) lateral and (**F**) medial views. All specimens to scale. Scale bar equals 5 cm.

is in obvious contrast to the reddish bones in purplish-red mudstone characterizing Brown's Burgersdorp and upper Elliot collections (Fig. 1). Although Barnard's Spruit cuts through both the lower and upper Elliot formations (E. Bordy pers. comm.), *Eucnemesaurus* (= '*Aliwalia*') is considered restricted to the lower Elliot based on subsequent discoveries of the taxon (McPhee *et al*. 2015). Thus, all available evidence indicates that the '*Aliwalia rex*' holotype and most of the rest of the 1876 lot originated in the lower Elliot Formation. The only specimens in the 1876 lot that do not appear to be from the lower Elliot Formation are a pair of *Lystrosaurus* skulls (NHMW 1876-VII-B-106, *L. declivis*, and NHMW 1876-VII-B-107, *L. murrayi*) preserved in a greenish-grey mudstone typical of the Early Triassic Katberg Formation (Groenewald 1996; Damiani *et al*. 2003).

Recent reexamination of the entirety of Brown's collection in Vienna has revealed that in addition to the '*Aliwalia*' femur and aforementioned jaw fragments, several clearly non-archosaurian elements are present among the materials of the 1876 lot. Remarkably, a number of these elements can be positively identified as belonging to a kannemeyeriiform dicynodont. Although dicynodonts are known from the Late Triassic of Europe (Dzik *et al*. 2008) and the Americas (Kammerer *et al*. 2013), dicynodont body fossils have never previously been reported from the Elliot Formation. There are, however, previous suggestions of a dicynodont in the lower Elliot based on the ichnofossil record. Ellenberger (1970, 1972) described a series of large, short-toed, pentadactyl tracks (*Pentasauropus incredibilis*) and identified the trackmaker as either a sauropod or dicynodont, with the latter identification supported by most subsequent authors (e.g. Olsen & Galton 1984; Anderson *et al*. 1998; D'Orazi Porchetti & Nicosia 2007). Hunt & Lucas (2007) admitted that the only obvious trackmaker for *Pentasauropus* is a dicynodont, but still questioned this identification because of the absence of dicynodont body fossils in the later Triassic (Norian–Rhaetian). The discovery of dicynodont remains among Brown's lower Elliot collections provides the first skeletal evidence for this clade in the Late Triassic of South Africa and supports the identification of *Pentasauropus* as a dicynodont track. The lower Elliot dicynodont is part of a surprisingly robust assortment of 'relictual' therapsid elements in this fauna (e.g. the large, herbivorous cynodonts *Scalenodontoides* and a *Diademodon*-like taxon; Gow & Hancox 1993; Abdala *et al*. 2007) and suggests that patterns of faunal replacement in the Late Triassic of southern Africa were more complex than previously thought.

MATERIALS AND METHODS

The following specimens were examined by the author for comparative purposes: *Angonisaurus cruickshanki* (NHMUK R9732); *Aulacephalodon bainii* (BP/1/766); *Daptocephalus leoniceps* (GPIT/RE/7176); *Dicynodon lacerticeps* (SAM-PK-K11431 [=B88 of Cluver & Hotton 1981]); '*Dicynodon tener*' (GPIT/RE/9642); *Dicynodontoides recurvidens* (SAM-PK-K6131); *Dinodontosaurus pedroanum* (MCN 3584; UFRGS PV0115T, PV0117T); *Ischigualastia jenseni* (MACN 18055; PVL 3807); *Jachaleria candelariensis* (UFRGS PV0147T, PV0150T); *Jachaleria colorata* (PVL 3841); '*Kannemeyeria*' *latirostris* (BP/1/3636); *Kannemeyeria lophorhinus* (BP/1/3638); *Kannemeyeria simocephalus* (BP/1/4524; ELM 1; FMNH UC 1514; NHMUK R3602, R3760; NHMW 1886-XV-4, 1886-XV-5; SAM-PK-3017; UCMP 42916; USNM 410298); *Moghreberia nmachouensis* (MNHN.ALM.38, ALM.80, ALM.167, ALM.280); *Placerias hesternus* (GPIT/RE/9578, 9582, 9585, 9588, 9590; MNA V2714, V2950, V8464; UCMP 24782, 24865, 24871, 24878, 25093, 25246, 25361, 25373, 25433, 27532, 32445, 32447; USNM 2198); *Sangusaurus parringtonii* (NMT RB42); *Sinokannemeyeria yingchiaoensis* (IVPP V974); *Stahleckeria potens* (AMNH FARB 7804; BSPG AS-XXV-14, AS-XXV-15; GPIT/RE/7106, 7107, 9599, 9600); *Tetragonias njalilus* (GPIT/RE/7110; UMZC T753); *Zambiasaurus submersus* (NHMUK R9039, R9040, R9098, R9109, R9113, R9140).

The phylogenetic analysis was run in TNT v1.1 (Goloboff *et al*. 2008) using New Technology search parameters (sectorial searching, parsimony ratchet, drift, and tree fusing) set to find minimum length at least 20 times. Support metrics were based on symmetric resampling using 10 000 replicates. The data matrix for this analysis is included as Supplementary material for this paper. The data matrix consists of 104 operational taxonomic units (mostly species-level anomodont taxa) and 197 characters, of which 23 are continuous and 174 are discrete. Continuous characters were treated as additive, following the method of Goloboff *et al*. (2006).

SYSTEMATIC PALAEONTOLOGY

Synapsida Osborn, 1903
Therapsida Broom, 1905
Anomodontia Owen, 1860
Dicynodontia Owen, 1860
Kannemeyeriiformes Maisch, 2001
Stahleckeriidae Lehman, 1961
Placeriinae King, 1988

***Pentasaurus goggai* gen. et sp. nov.**

LSID. urn:lsid:zoobank.org:pub:71989008-7163-4267-BD31-8023AB826FFE

Holotype. NHMW 1876-VII-B-114, a partial mandible. Given the lack of overlapping elements and comparable sizes of all the referred material, it is probable that all of these elements represent a single individual. In the absence of detailed collection information this must be considered speculative, however, particularly given the past history of chimaerical associations from this locality.

Referred material. NHMW 1876-VII-B-115, a partial left ulna; NHMW 1876-VII-B-121, a partial left scapulocoracoid; NHMW 1876-VII-B-122, a partial left pubis and ischium; NHMW 1876-VII-B-123, the distal end of a left humerus; NHMW 1876-VII-B-128, the proximal tip of a right tibia; NHMW 1876-VII-B-129, a partial long bone (?radius); NHMW 1886-XV-15, a partial cervical vertebra.

Type locality and horizon. Probably Barnard's Spruit (per Galton & Van Heerden 1998), ~24 kilometres south of

Aliwal North, Eastern Cape Province, South Africa. Lower Elliot Formation, Stormberg Group, Karoo Supergroup; Late Triassic.

Etymology. From the ichnogenus *Pentasauropus* Ellenberger, 1970, in a reversal of the historical tendency to name tetrapod track ichnogenera by appending the suffix '*-pus*' (meaning 'foot') to the generic stem of the supposed trackmaker (e.g. *Anchisauripus*, *Dicynodontipus*, *Megalosauropus*). Named in reference to its status as the probable trackmaker of the *Pentasauropus* tracks from the lower Elliot Formation. Species named in honor of its collector, Alfred Brown (1834–1920), nicknamed 'Gogga' (pronounced 'χɒχə [IPA]; Afrikaans for 'bug') in reference to his eccentric habits. Initially derogatory, this nickname was later celebrated (Drennan 1938). Brown was greatly disappointed in the lack of attention given to his discoveries by European researchers; this species name may be taken as extremely belated recognition of his collection efforts on behalf of the Imperial Natural History Museum of Austria-Hungary.

Diagnosis. Distinguished from all other known dicynodonts by the morphology of the lateral dentary shelf (highly discrete and robust, nearly straight, and positioned very anteriorly on the dentary ramus, with no apparent contact with the mandibular fenestra). Distinguished from non-stahleckeriid dicynodonts by the remarkably large contribution of the splenial to the anteroventral face of the jaw symphysis. Distinguished from non-placeriine stahleckeriids by the relatively tall, steeply-sloping mandibular symphysis and the presence of a midline ridge on the anteroventral face of the symphysis. In addition to the aforementioned morphology of the lateral dentary shelf, distinguished from *Placerias* by the generally broader symphysis with more rounded edges, shallower mid-dentary groove on the dorsal surface of the symphysis, larger, rounder dentary table, and absence of accessory grooves lateral to the midline symphysial ridge. Based on referred elements, further distinguished from all other dicynodonts by the extreme robusticity of the distal humerus (greatly anteroposteriorly expanded) and the presence of paired rugosities on the posterolateral margin of the frontals.

DESCRIPTION

NHMW 1876-VII-B-114. Holotype. A partial mandible preserving the symphysis (missing the tip of the beak) and part of the left mandibular ramus (Figs 3A, 4A, 5B, 6, 7A, 8E). This is a large, fused element unmistakably dicynodontian in morphology. The anterior face of the symphysis is 15.1 cm high and 9.7 cm wide. Dorsally, the mid-dentary groove is very shallow compared to other kannemeyeriiforms, even *Placerias* (a taxon in which the mid-dentary groove is already shallower than in stahleckeriines or kannemeyeriids; Fig. 3B). Lateral to the mid-dentary groove are paired dentary tables (*sensu* Angielczyk & Rubidge 2013; Fig. 3A). The right dentary table is worn but the left is intact and well preserved. It is a rounded structure, flattened dorsally, similar in morphology to that of *Stahleckeria* (Fig. 7C) but transversely broader than that of *Placerias* (Fig. 3B). It is separated by a short depression from the raised edge of the dentary that would surround the posterior dentary sulcus anterolaterally (the sulcus itself is not preserved). The anteroventral face of the jaw symphysis bears a well-developed midline ridge (Fig. 4A). This ridge is most prominent at the dorsal edge of the symphysis, sloping downwards posteroventrally and seemingly terminating before the suture with the splenial (although damage in this region makes this somewhat uncertain). This morphology differs sharply from that of *Kannemeyeria*, in which the ridge is longer (potentially correlated with the proportionally shorter splenial in that taxon) and flanked on both sides by elongate symphysial grooves (Figs 4B, 5E). It also differs from *Placerias*, in which the midline ridge is similar in position and morphology but is also flanked by well-developed accessory grooves. These grooves extend far enough ventrally in *Kannemeyeria* and *Placerias* that their absence in NHMW 1876-VII-B-114 cannot be explained solely by loss of the beak tip in this specimen. The jaw symphysis of *Pentasaurus* further differs from that of *Placerias* in being proportionally broader (Figs 3A, 4A) and gently rounded between its anterior and lateral faces, unlike the sharp edges between these surfaces in *Placerias* and *Stahleckeria* (Fig. 5C,F).

The lateral dentary shelf is preserved on the left mandibular ramus (Figs 6, 7A). The shelf is nearly horizontal for most of its length, but curves slightly dorsally at its posterior end. It is remarkably robust and situated unusually far forward on the jaw compared to the condition in other kannemeyeriiforms (Fig. 7). In most dicynodonts the lateral dentary shelf is intimately associated with the mandibular fenestra (King 1988); in NHMW 1876-B-VII-114 there is no clear evidence of the mandibular fenestra being preserved, yet a clear posterior terminus of the lateral dentary shelf appears to be present. The atypical morphology of this structure raises the question of whether it represents a lateral dentary shelf at all or could be an affixed, unrelated bone fragment. However, careful examination of this specimen indicates that this structure is indeed contiguous with the rest of the jaw. It may have been somewhat distorted by taphonomic processes (its anterior tip is highly abrupt and appears damaged), but does appear to represent a natural part of the jaw bone.

The splenial makes a very large contribution to the ventral portion of the symphysis, as is typical of dicynodontoids in general and stahleckeriids in particular (Fig. 5). It is extremely broad at the base of the symphysis, but attenuates in width anterodorsally before ending at a point ventral to the terminus of the midline dentary ridge. The anteroventral face of the splenial is worn, so it is uncertain whether any surface ornamentation (ridges, etc.) was present on this element. Posterolateral to the splenial, the anterior tip of the angular is preserved on the left side of the specimen. The preserved portion of the angular is attenuate, but remarkably broad compared to that of non-stahleckeriid dicynodonts (compare Fig. 5B, C,F with Fig. 5A,D).

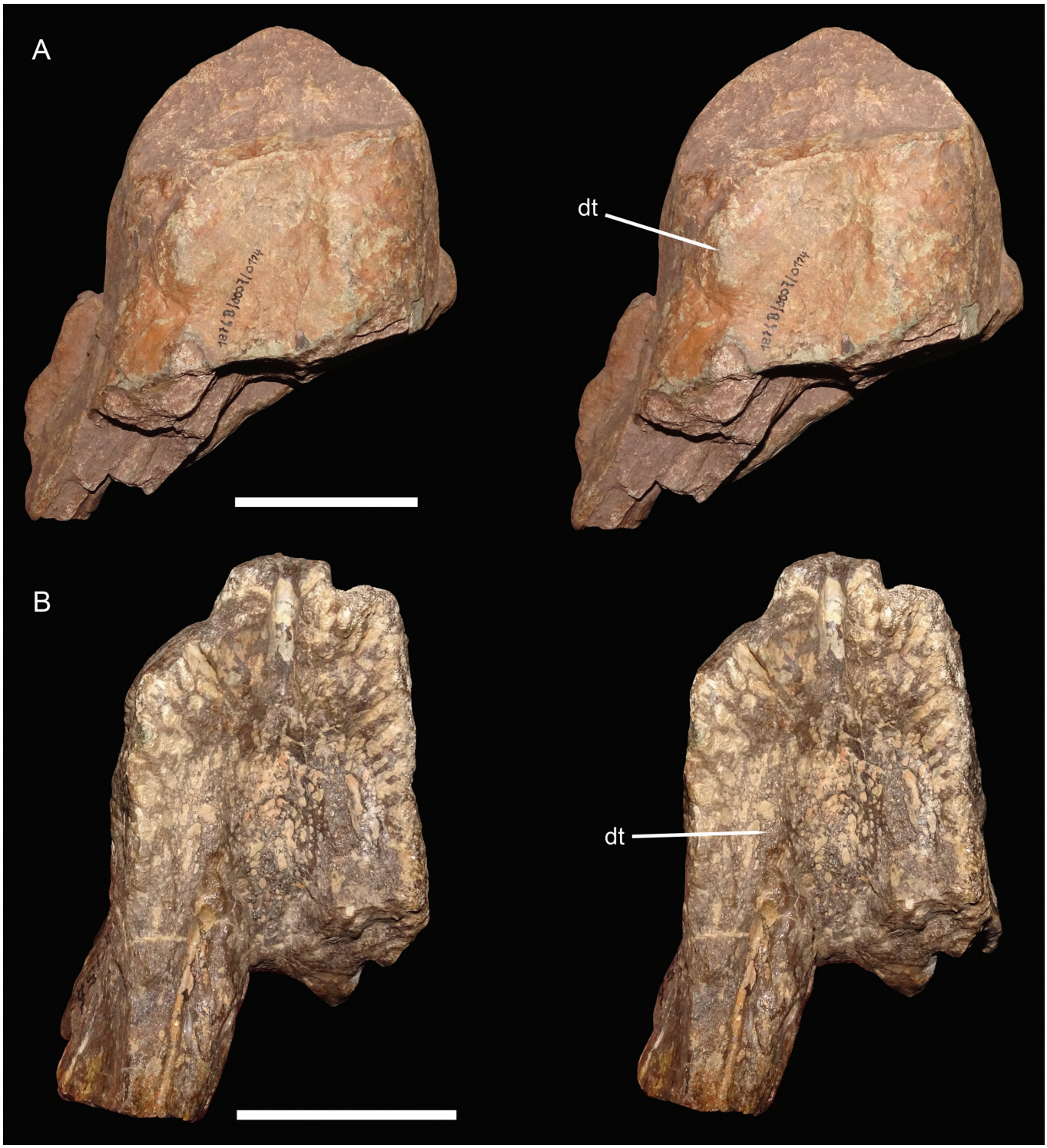

Figure 3. Stereopairs of kannemeyeriiform mandibles in dorsal view: **A**, *Pentasaurus goggai* (NHMW 1876-VII-B-114); **B**, *Placerias hesternus* (GPIT/RE/9578). dt, dentary table. Anterior is up. Scale bars equal 5 cm.

NHMW 1876-VII-B-115. The proximal portion of a left ulna (Fig. 8A–C), maximum length 14.8 cm. The radial notch is well preserved (Fig. 8B,C), and the bases of the lateral and coronoid processes are also preserved, although their tips are worn off. In general, this element is badly worn but is similar in morphology to that of *Stahleckeria* (Fig. 8D,E). Poor preservation makes it difficult to determine whether the olecranon was fused with the ulna or was a separate element, as is the case in some other kannemeyeriiforms. A separate olecranon is present in *Placerias* (Camp & Welles 1956) and *Ischigualastia* (Cox 1965), but it is fused with the ulna in most specimens of *Stahleckeria* (Huene 1935). However, at least some *Stahleckeria* specimens lack a fused olecranon (Fig. 8D,E), suggesting that fusion of this element could be variable within stahleckeriid taxa. Because the tip of the ulna in NHMW 1876-VII-B-115 appears to be rounded and worn but not clearly broken, it is likely that the olecranon was not fused in this particular specimen.

NHMW 1876-VII-B-118. A cranial fragment of maximum width 10.8 cm (Fig. 9A,C). This element is interpreted as

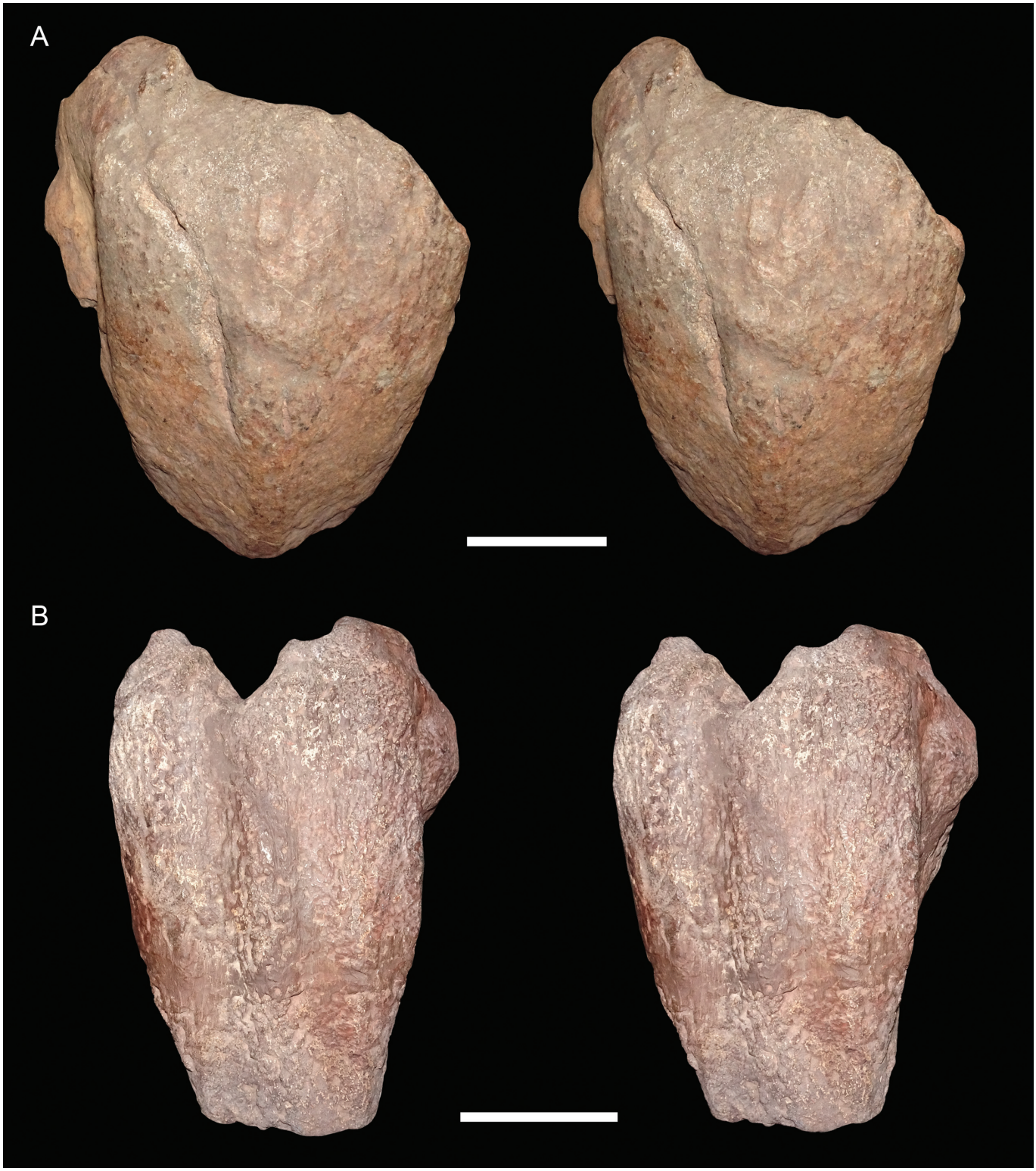

Figure 4. Stereopairs of kannemeyeriiform mandibles in anteroventral view: **A**, *Pentasaurus goggai* (NHMW 1876-VII-B-114); **B**, *Kannemeyeria simocephalus* (NHMW 1886-XV-5). Anterior is down. Scale bars equal 5 cm.

part of the skull roof at the anterior edge of the intertemporal region, consisting of portions of both frontals, the left postorbital, and the prearietal. The left ventrolateral edge of the element is markedly curved and bears an elongate, prominent dorsal depression, which is interpreted as the muscle attachment site for the adductor mandibulae on the postorbital. A large channel cuts through this element at its posterior edge, which is interpreted as the pineal foramen. The bone surface immediately anterior to this foramen is depressed, where the prearietal would be in other kannemeyeriiforms (sutures are difficult to discern because of incomplete preparation, but their interpreted locations are shown in Fig. 9A). Outside of the depressed regions, the bone surface is notably rugose. In particular, there are paired, mound-like rugosities on the frontals at their borders with the postorbitals (the right postorbital is not preserved, and this rugosity projects freely at the edge of the specimen;

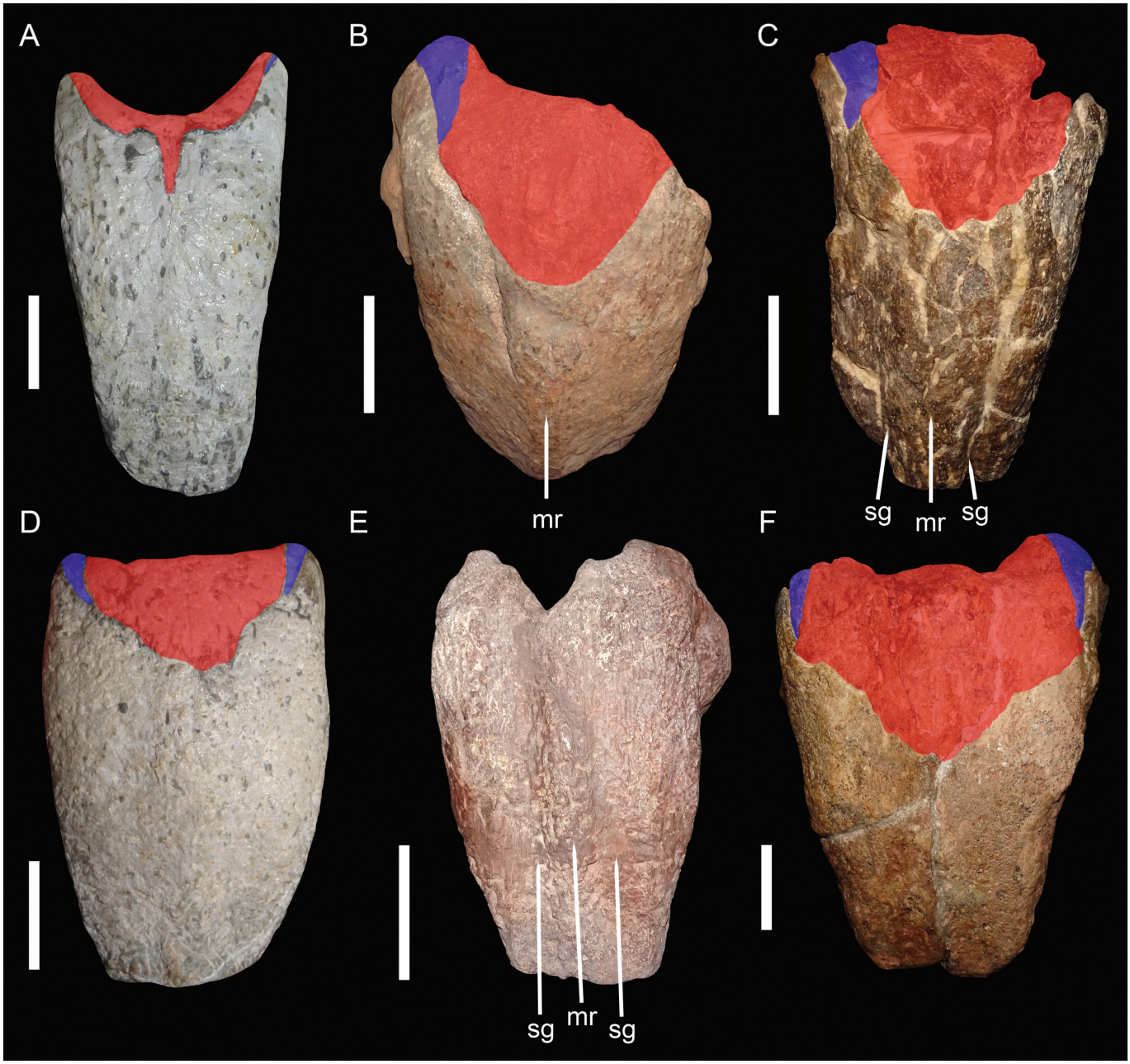

Figure 5. Dicynodont mandibles in anteroventral view, showing variation in symphysial composition and ornamentation: **A**, *Dicynodontoides recurvidens* (SAM-PK-K6131), representative of the non-dicynodontoid condition; **B**, *Pentasaurus goggai* (NHMW 1876-VII-B-114); **C**, *Placerias hesternus* (GPIT/RE/9578), a placeriine stahleckeriid; **D**, *Dicynodon lacerticeps* (SAM-PK-K11431), representative of the non-kannemeyeriiform dicynodontoid condition; **E**, *Kannemeyeria simocephalus* (NHMW 1886-XV-5), a kannemeyeriiform dicynodontoid; **F**, *Stahleckeria potens* (GPIT/RE/7107), a stahleckeriine stahleckeriid. Splenials are highlighted in red and angulars in blue (only the dentary is preserved in **E**, but rough dimensions of the splenial can be determined from the empty, triangular notch at top of figure). Note enlargement of the splenial contribution to the symphysis in dicynodontoids compared to non-dicynodontoid dicynodonts (**A**), extreme enlargement of the splenial in stahleckeriid kannemeyeriiforms (**B**, **C** and **F**), and greater contribution of the angular to the symphysis in kannemeyeriiforms. Also note variability in ornamentation on the anterior face of the symphysis: a median ridge is absent in *Dicynodontoides*, *Dicynodon* and *Stahleckeria*, present but confined to the dorsal tip of the symphysis in *Pentasaurus* and *Placerias*, and present along the entire symphysial midline in *Kannemeyeria*. The median ridge is surrounded by a pair of well-developed grooves also running along the length of the symphysis in *Kannemeyeria*, whereas the accessory grooves are short and also restricted to the tip of the symphysis in *Placerias*. No accessory grooves are present in *Pentasaurus*. mr, median ridge; sg, symphysial groove. Anterior is down. Scale bars for **A** and **D** equal 1 cm, whereas those for **B**, **C**, **E**, and **F** equal 5 cm.

see Fig. 9A). Paired rugosities in this region are not known in other kannemeyeriiforms (e.g. Fig. 9B,D) and may be an autapomorphy of *Pentasaurus*, although the circumorbital region of *Placerias* is generally also very rugose (Kammerer *et al*. 2013). The ventral surface of the postorbital-frontal region curves ventromedially (Fig. 9C). Along the ventral midline of the element is a narrow channel between the frontals that would house part of the dorsal margin of the brain (Camp & Welles 1956).

NHMW 1876-VII-B-121. A partial left scapulocoracoid, consisting of the circum-glenoid region (Fig. 10A). This fragment as a whole is 19.5 cm in maximum length, with the base of the scapular spine being 10.2 cm in width and

Figure 6. Stereopair of the holotype jaw of *Pentasaurus goggai* (NHMW 1876-VII-B-114) in left lateral view. Anterior is up. Scale bar equals 5 cm.

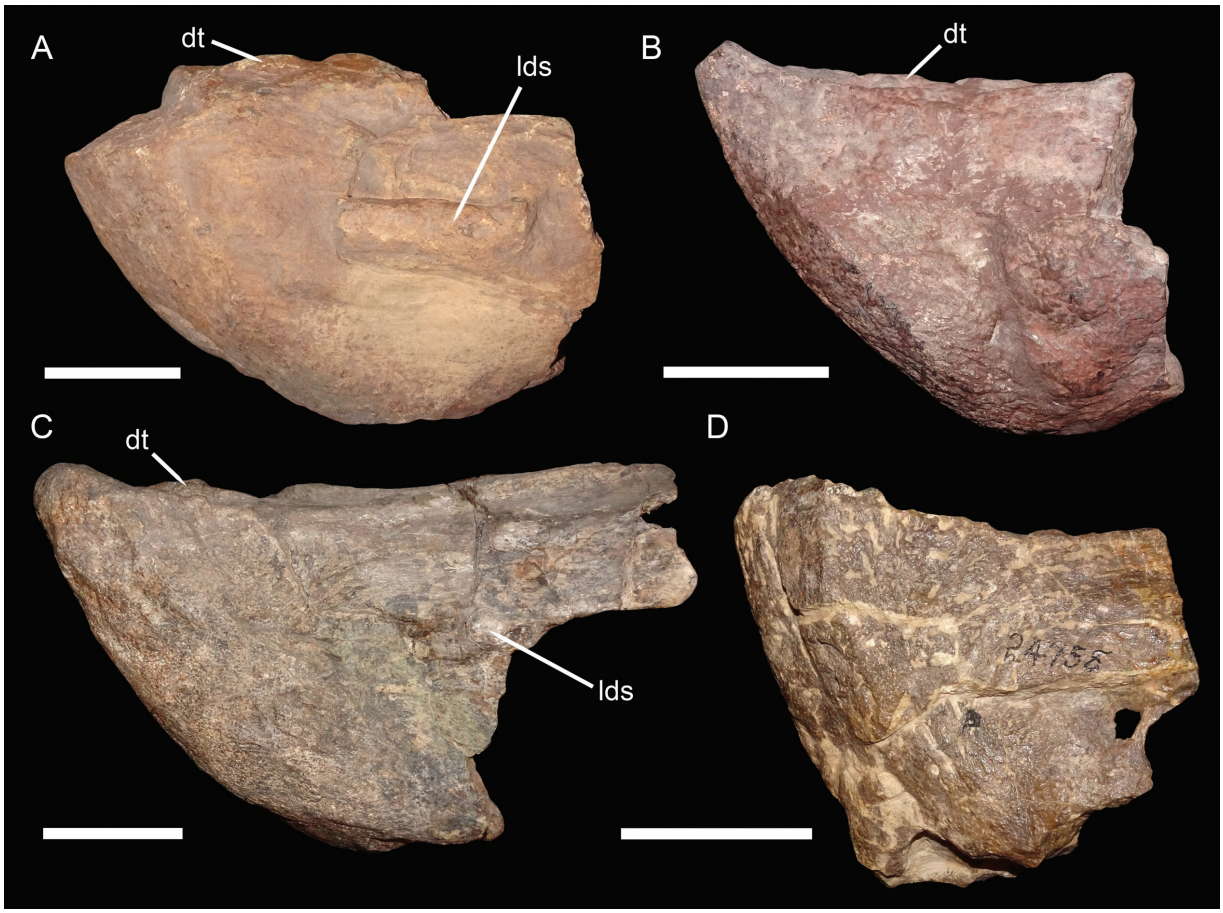

Figure 7. Anterior portions of kannemeyeriiform mandibles in lateral view: **A**, *Pentasaurus goggai* (NHMW 1876-VII-B-114); **B**, *Kannemeyeria simocephalus* (NHMW 1886-XV-5); **C**, *Stahleckeria potens* (GPIT/RE/7106); **D**, *Placerias hesternus* (GPIT/RE/9578). Note autapomorphic robust lateral dentary shelf at unusually anterior position on dentary in **A**; comparable structure absent in this position and of smaller size in other taxa. Specimens in **A**, **C**, and **D** in left lateral view, **B** in right lateral view but mirrored for comparative purposes. dt, dentary table; lds, lateral dentary shelf. Scale bars equal 5 cm.

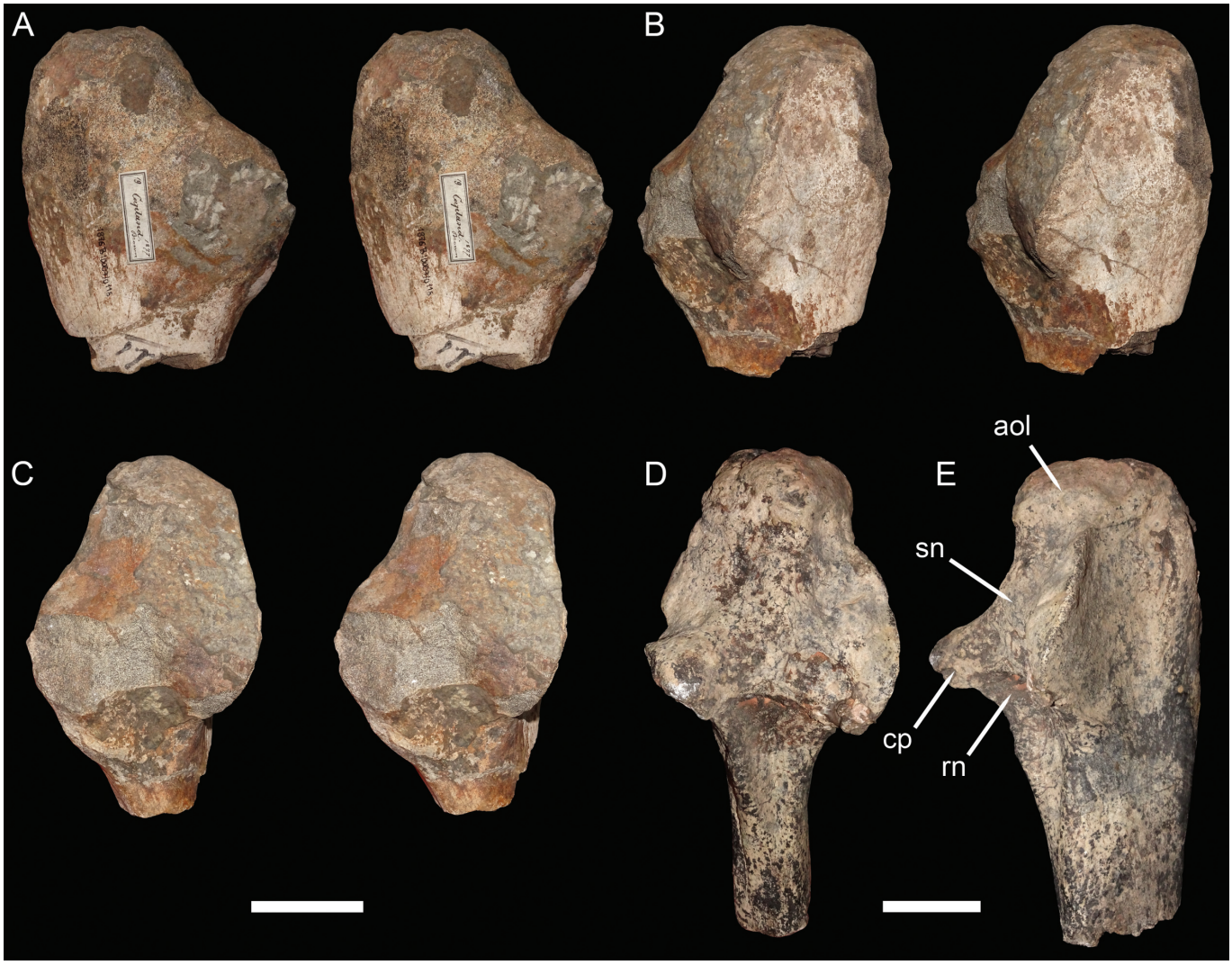

Figure 8. Ulna of *Pentasaurus goggai* (NHMW 1876-VII-B-115) and comparison with *Stahleckeria*. Stereopairs of proximal portion of left ulna in (**A**) posterior, (**B**) anterior, and (**C**) proximodorsal views. Proximal portion of right ulna (mirrored for comparison) of *Stahleckeria potens* (GPIT/RE/9600) in (**D**) proximodorsal and (**E**) anterior views. aol, point of articulation with unfused olecranon; cp, coronoid process; rn, radial notch; sn, sigmoid notch. Different views of single specimens to scale with one another. Scale bars equal 5 cm.

the glenoid fossa being 10.0 cm in height. Although poorly preserved, this element can be recognized as dicynodont and not sauropodomorph or 'rauisuchian' by the close proximity of the procoracoid foramen to the glenoid fossa, the strongly posterolaterally-oriented glenoid (more posteriorly-oriented in sauropodomorphs and 'rauisuchians', related to their upright gait), and the large size of the glenoid relative to the scapular width. The procoracoid foramen is a large (2.5 × 1.0 cm), ovoid opening entirely surrounded by the procoracoid, which is situated anterior to the glenoid fossa and separated from it by a distance of 3.3 cm. The procoracoid is excluded from the glenoid by a narrow contact between the coracoid and scapula. The posterior margin of the coracoid is strongly concave immediately ventral to the rim of the glenoid, as in other stahleckeriids (Fig. 10B). Unfortunately, the scapula is broken beyond the glenoid rim, so it is unknown whether a tricipital tubercle was present.

NHMW 1876-VII-B-122. A lot made up of two bones, a partial left pubis (10.7 cm maximum preserved length) and ischium (10.1 cm maximum preserved length). The dorsal and ventral edges of the pubis (Fig. 11A,B) are badly worn, but the central shaft is well-preserved and exhibits the sharp 'twisting' typical of kannemeyeriiforms (Fig. 11G). The ischium (Fig. 11D,E) is highly incomplete, and consists of a thick, worn edge of the acetabulum and a thinning lamina extending ventrally.

NHMW 1876-VII-B-123. The distal end of a left humerus (Figs 12, 13, 14A, 15A, 16A), with the maximum width across the entepi- and ectepicondyles being 15.5 cm. This element is broken at mid-shaft. The preserved base of the deltopectoral crest indicates that it was oriented at a nearly 90º angle relative to the long axis of the distal edge of the humerus (Fig. 16A), similar to that of *Placerias* (Camp & Welles 1956). A large, ovoid entepicondylar foramen pierces the ridge running proximally from the base of the deltopectoral crest, as is typical for therapsids. Its exit on the ventral face of the humerus is not visible due to plaster reconstruction. The entepicondyle is damaged, with part of its tip worn off. However, the sharp slope of the preserved portion of the entepicondyle indicates that little more of this structure would have been present, and

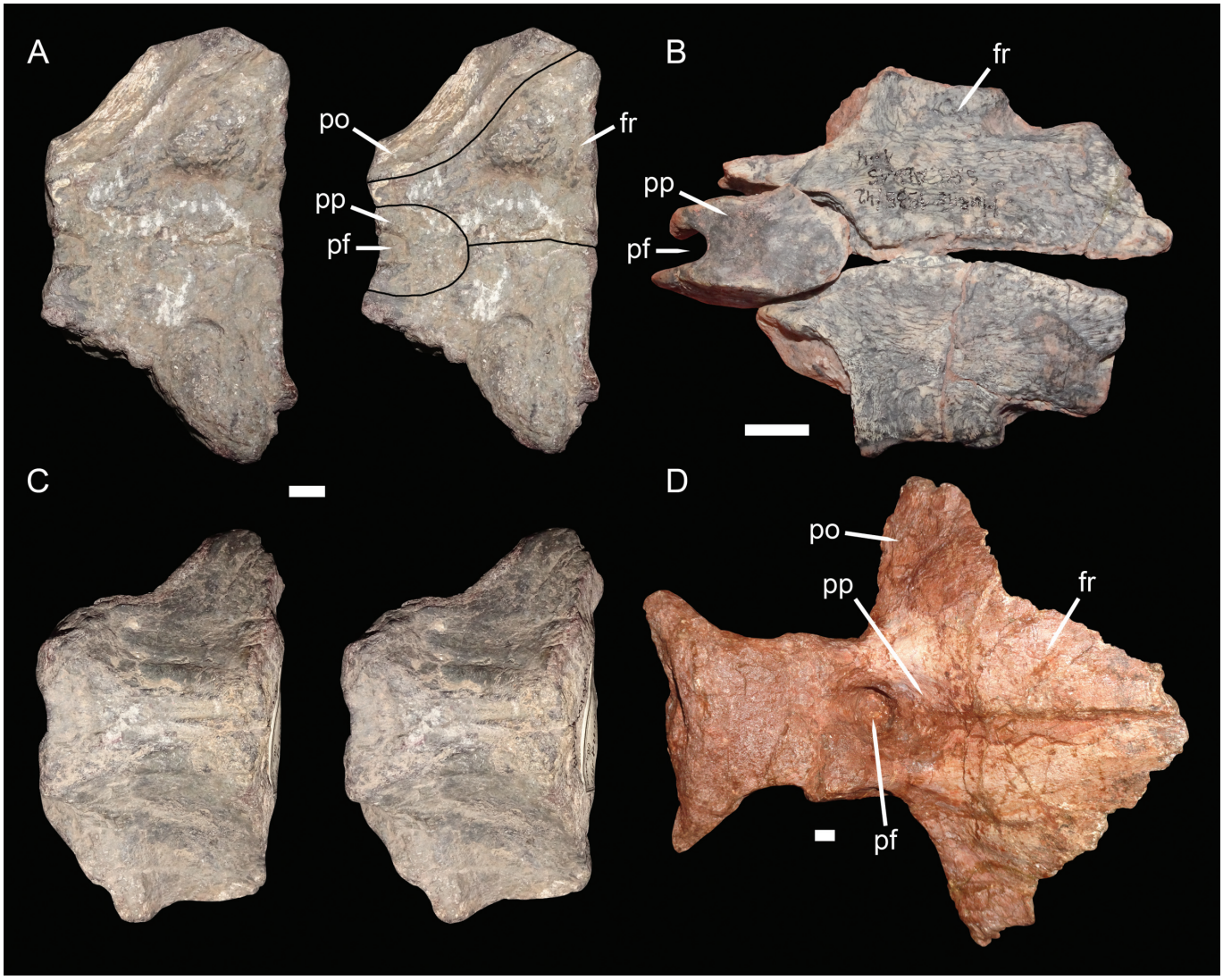

Figure 9. Skull roof fragment of *Pentasaurus goggai* (NHMW 1876-VII-B-118) and comparisons with other kannemeyeriiforms. Stereopairs of intertemporal fragment in (**A**) dorsal (with interpretive drawing of sutures) and (**C**) ventral views. **B**, *Dinodontosaurus* (lectotype of *Dicynodon tener*; GPIT/RE/9642) partial skull roof (disarticulated preparietal and frontals) in dorsal view; **D**, *Moghreberia nmachouensis* (MNHN.ALM.280) intertemporal bar and partial interorbital region in dorsal view. fr, frontal; pf, pineal foramen; po, postorbital; pp, prepariental. Anterior is right for all specimens. Scale bars equal 1 cm.

its total extent would have been similar to that of *Zambiasaurus* (Fig. 14C). In general, the entepicondyle and ectepicondyle would have been relatively short, like those of other placeriines (Fig. 14B,C), and unlike the extremely anteroposteriorly broad condyles of stahleckeriines (Fig. 14D). On the anterior edge of the distal humerus is a very tall, subvertical supinator process (Figs 13, 14A), which is characteristic of placeriines (Kammerer *et al*. 2013; see also Fig. 14B,C) and differs sharply from that of stahleckeriines, in which the supinator process is a tab-like structure occupying a more restricted region (Fig. 14D). The supinator process of *Pentasaurus* originates near the base of the humeral shaft and curves proximodorsally to distoventrally, terminating near the distal tip of the ectepicondyle (Fig. 13); it is not distinctly separated from the ectepicondyle as in stahleckeriines and numerous other Permo-Triassic amniotes (Romer 1956). The tip of the ectepicondyle of *Pentasaurus* is angled anteroventrally (Fig. 15A), as in *Zambiasaurus* (Fig. 15C) and unlike *Placerias* and *Stahleckeria* in which it is angled anterodorsally (Fig. 15B, D). The tip of the entepicondyle is angled posterodorsally (Fig. 15A), as in *Placerias* and *Zambiasaurus* (Fig. 15B,D) but unlike *Stahleckeria* in which it is only weakly angled, but somewhat posteroventrally (Fig. 15D).

The distal face of the humerus is massive, being very dorsoventrally thick even compared to that of other stahleckeriids (Fig. 15). The capitulum is mostly unossified and would have had a thick cartilage cap in life. This is the condition in most dicynodont humeri, including *Zambiasaurus* (Figs 14C, 15C), but a well-ossified capitulum with a bulging, rounded surface is present in *Placerias* (Figs 14B, 15B), stahleckeriines (Figs 14D, 15D), and some other kannemeyeriiforms (e.g. *Angonisaurus*, NHMUK R9732; *Dinodontosaurus*, MCN 3584; *Sinokannemeyeria*, IVPP V974). Greater ossification of the distal humerus occurs ontogenetically in therapsids (Kemp 1986), and the unossified state of the capitulum in this specimen (and the known *Zambiasaurus* humeri) may be indicative of immaturity (although comparably-sized *Placerias* humeri are well-ossified; USNM 2198, the holotype of *P. hesternus*, is 16.8 cm across at its distal end and has a prominent bony capitulum). Posterior to the capitulum on

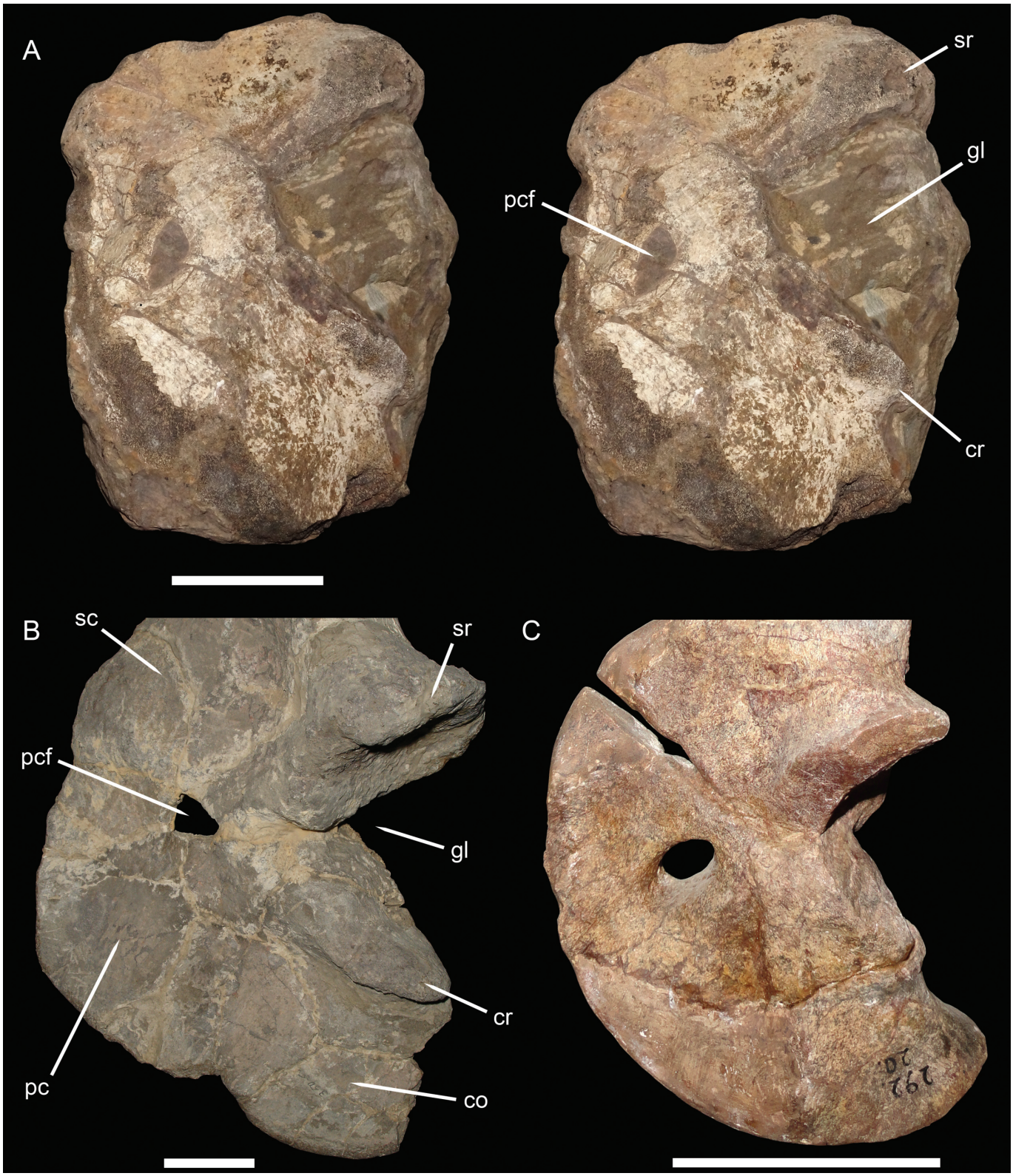

Figure 10. Scapulocoracoid of *Pentasaurus goggai* (NHMW 1876-VII-B-121) and comparisons with other kannemeyeriiforms. (**A**) Stereopair of partial scapulocoracoid, preserving circum-glenoid region. **B**, *Ischigualastia jenseni* (MACN 18055); **C**, *Tetragonias njalilus* (GPIT/RE/7110). All specimens represent left scapulocoracoids in lateral view. co, coracoid; cr, coracoid rim of glenoid; gl, glenoid fossa; pc, procoracoid; pcf, procoracoid foramen; sc, scapula; sr, scapular rim of glenoid. Scale bars equal 5 cm.

the ventral face of the humerus is the trochlea (the articular surface for the ulna; Fig. 14A), which extends across the distal humeral surface (Fig. 15A). Opposite the capitulum, on the dorsal face of the humerus, is a deep and well-developed intercondylar groove, which surrounds the terminus of the trochlea (Figs 12B, 15A). Extension of the trochlea onto the dorsal humeral surface is usually the case in kannemeyeriiforms, correlated with depression of the humerus below the level of the glenoid fossa and resulting in the body being held higher off the ground than in earlier dicynodonts (Ray 2006).

NHMW 1876-VII-B-128. The proximal end of a right tibia (Figs 16B, 17A, C), 10.8 × 9.4 cm across the proximal face.

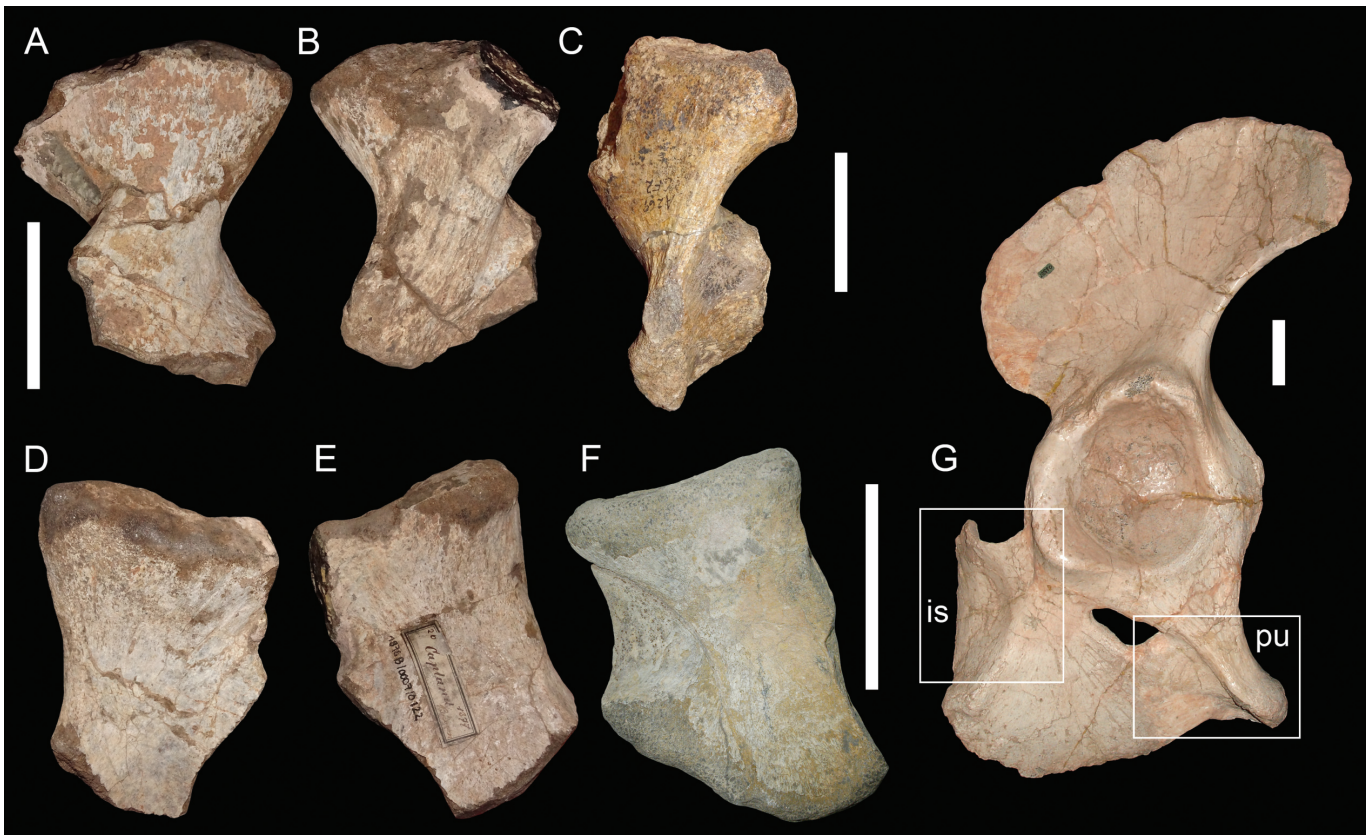

Figure 11. Pelvic elements of *Pentasaurus goggai* (NHMW 1876-VII-B-122) and comparisons with other stahleckeriids. Fragment of left pubis in (**A**) medial and (**B**) lateral views. Fragment of left ischium in (**D**) medial and (**E**) lateral views. **C**, *Placerias hesternus* (GPIT/RE/9585), isolated left pubis fragment in lateral view. **F**, *Zambiasaurus submersus* (NHMUK R9109), isolated left ischium fragment in lateral view. **G**, *Jachaleria candelariensis* (UFRGS PV0150T), nearly complete right pelvis in lateral view, highlighting the regions preserved in NHMW 1876-VII-B-122. Note strong 'twisting' of the pubis in **B**, **C**, and **G**. is, ischium; pu, pubis. **A**, **B**, **D**, and **E** to scale. Scale bars equal 5 cm.

The proximal surface bears a depressed articular surface broken into two sulci (lateral and medial), for contact with the distal condyles of the femur (Fig. 17C). A well-developed groove (the incisura tibialis) is present posterior to the cnemial crest. Unfortunately, the cnemial crest and medial sulcus are badly damaged, although what is preserved is generally consistent with that of *Placerias* (Fig. 17B,D). The medial sulcus is broader than the lateral, as is typical of kannemeyeriiforms (Camp & Welles 1956). Given the very incomplete nature of this element, the possibility that it could also be from a sauropodomorph must be carefully considered. However, in Triassic sauropodomorph tibiae the proximal condyles are typically more prominently projecting (Martínez & Alcober 2009; Apaldetti *et al*. 2013) than is the case in NHMW 1876-VII-B-128. Furthermore, a natural cross-section through this element (Fig. 16B) reveals that it has a thinner outer layer of cortical bone than in sauropodomorphs and is extensively filled with trabecular bone, which is typical for Triassic dicynodonts (Chinsamy 1993; Botha-Brink & Angielczyk 2010).

NHMW 1876-VII-B-129. The fragmentary, incompletely prepared tip of a long bone (Fig. 18) of appropriate size (shaft diameter 4.9 cm) and with preservation style according with the other elements listed here. Rough proportions and the presence of a ridge running down the shaft on one side of the bone suggest that it may be a radius, but this is uncertain.

NHMW 1886-XV-15. A worn, isolated vertebra missing the neural spine (Fig. 19A–C,F,G). Maximum height from the base of the centrum to the base of the (broken) neural spine is 9.1 cm, transverse width of the centrum is 5.7 cm, and anteroposterior length of the centrum is 3.6 cm. The vertebra is amphicoelous. The pre- and postzygapophyses are broken off; their positions and rough proportions are comparable to those of other kannemeyeriiforms (Fig. 19). The transverse processes (=diapophyses) are short; although their tips are worn they could not have extended much further than preserved. Given the poor preservation of this specimen, it is difficult to be certain where in the axial column this vertebra originated. Cervical and dorsal vertebrae in kannemeyeriiforms are generally similar and these series grade into each other (Cruickshank 1975), so can be hard to tell apart when isolated. In general, however, kannemeyeriiform cervical vertebrae have anteroposteriorly and transversely narrower and dorsoventrally taller neural spines and stronger curvature of the ventral surface of the centrum than dorsals (Fig. 19; see also Pearson 1924; Huene 1935; Bandyopadhyay 1988). The length of the transverse process varies extensively along the length of the vertebral column (King 1988), but is usually shorter in the cervicals than the anterior dorsals. The position of the parapophysis also shifts along the length of the axial column: in anterior cervicals, the parapophysis is located low on the anterior edge of the centrum (Fig. 19I), but it is situated higher (near centrum mid-height) on posterior

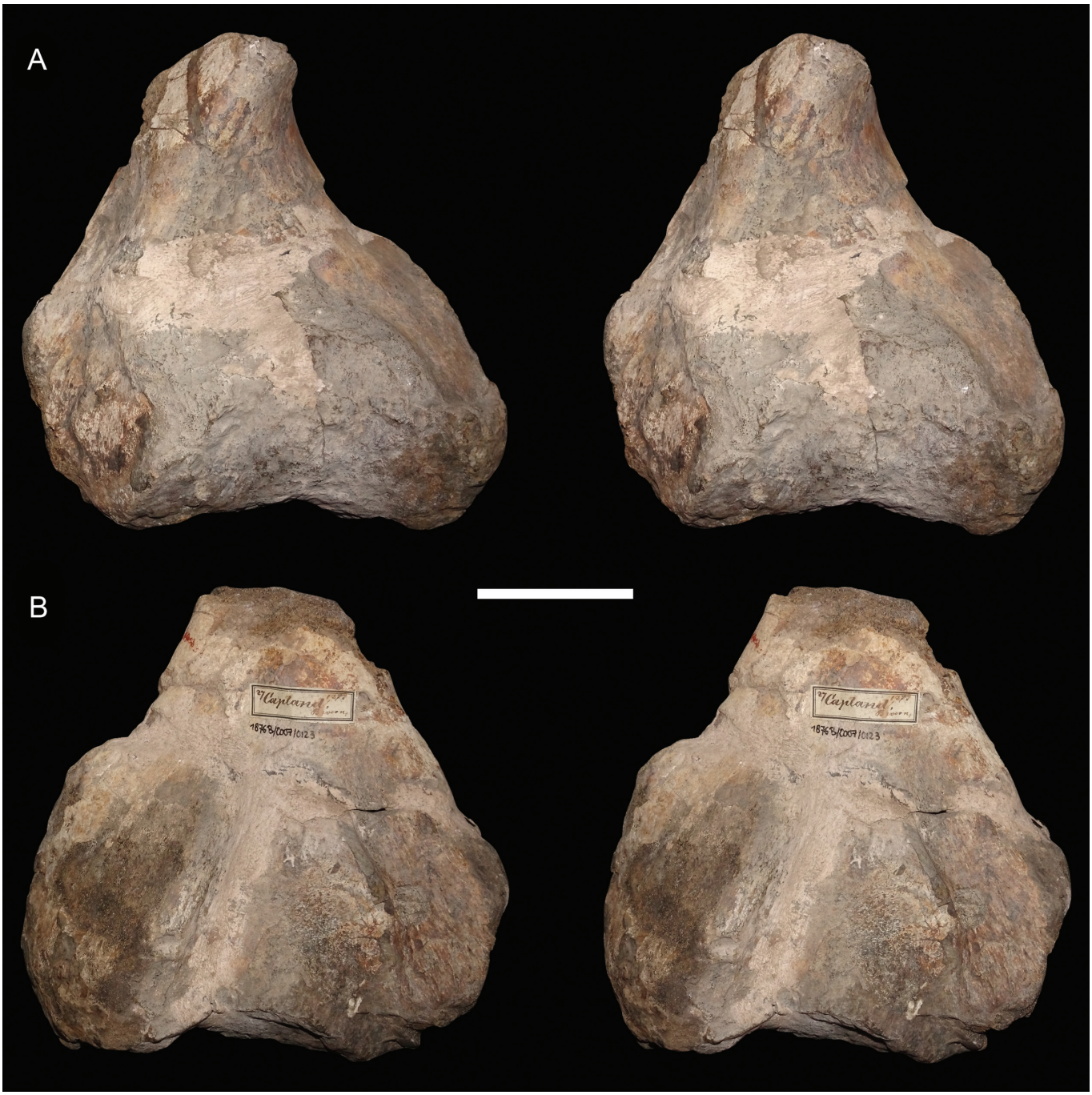

Figure 12. Stereopairs of NHMW 1876-VII-B-123, distal portion of left humerus of *Pentasaurus goggai*, in (**A**) ventral and (**B**) dorsal views. Scale bar equals 5 cm.

cervicals and higher still (at the anterodorsal corner of the lateral surface of the centrum) on anterior dorsals (Fig. 19H). In posterior dorsals a distinct parapophysis is absent, as it fuses to the base of the transverse process to form a synapophysis (Bandyopadhyay 1988). Although it is difficult to see because of wear, there appears to be the base of a parapophysis low on the centrum in NHMW 1886-XV-15 (Fig. 19F). Combined with the relatively concave ventral surface of the centrum, short transverse processes, and large neural canal, this suggests that this specimen represents a cervical vertebra. Note that this specimen is one of a few of Brown's lower Elliot fossils accessioned in the later NHMW lot (1886, instead of 1876), another being the proximal portion of the holotype femur of *'Aliwalia rex'* (1886-XV-39; misnumbered 1889-XV-39 by Galton & van Heerden [1998], Yates [2007], and McPhee *et al*. [2015]).

PHYLOGENETIC ANALYSIS

Pentasaurus goggai was included in the most recent available phylogenetic data set for anomodonts, that of Angielczyk & Kammerer (2017). Codings were based on the holotype and all referred material. Three additional characters were added to the Angielczyk & Kammerer (2017) matrix to incorporate information pertinent for subfamily-level identification of *Pentasaurus*:

172. Anterior face of dentary symphysis: 0, unornamented; 1, with median ridge.

Primitively, the dentary symphysis of dicynodonts has a

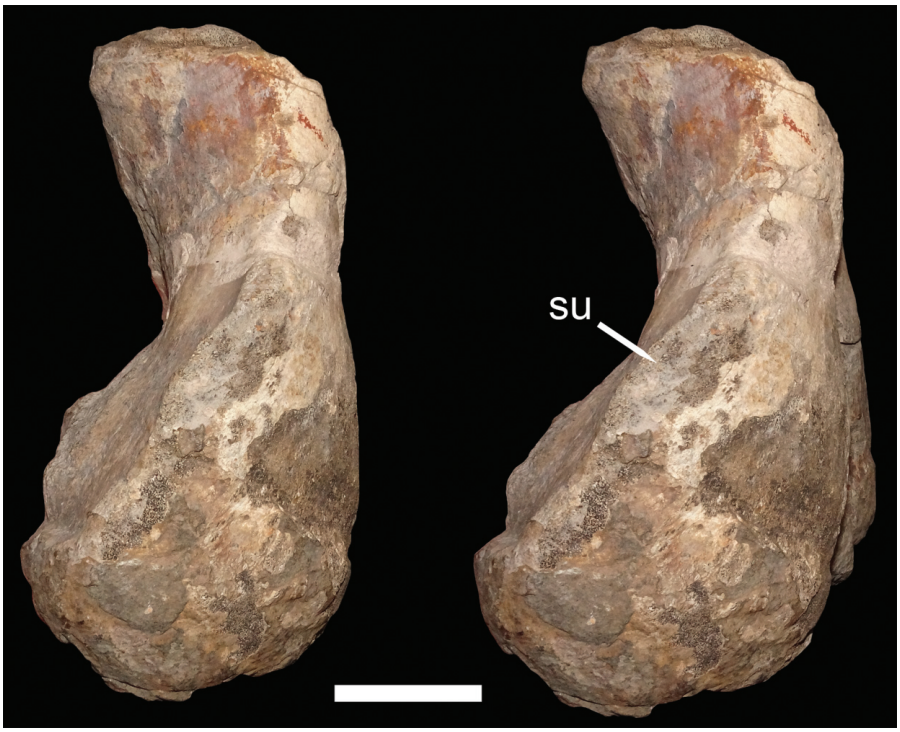

Figure 13. Stereopair of NHMW 1876-VII-B-123, distal portion of left humerus of *Pentasaurus goggai*, in anterior view. su, supinator process. Scale bar equals 5 cm.

weakly convex anterior face, but no distinct ridges or grooves. Some late Permian and most Triassic dicynodonts, however, have a well-developed midline ridge on the symphysial surface, sometimes bounded laterally by accessory grooves. The length of the ridge varies between taxa: in some (like *Lystrosaurus*) it is restricted to the dorsal portion of the symphysis, whereas in others (like *Kannemeyeria*) it extends down the entire length of the symphysis. Among cryptodonts, a midline ridge is present in geikiids and *Oudenodon*, but not *Tropidostoma*, *Australobarbarus*, or rhachiocephalids. A midline ridge is present in most dicynodontoids, albeit not 'elphids' (if indeed they are dicynodontoids), *Gordonia*, *Jimusaria*, *Vivaxosaurus*, and *Dicynodon* proper. Within Kannemeyeriiformes, the stahleckeriines *Sangusaurus*, *Stahleckeria*, *Ischigualastia*, and *Jachaleria* are unusual in lacking a midline ridge (no mandibular material is known for *Eubrachiosaurus*).

173. Supinator process above ectepicondyle of humerus: 0, absent; 1, present.

The supinator process is a bony ridge on the anterior edge of the distal humerus, proximal to the ectepicondyle, which serves as an attachment site for the supinator muscle (Romer 1956). This process is present in many early amniotes, and although ancestrally absent as a discrete structure in therapsids (Hopson & Barghusen 1986), it re-evolved several times in various dicynodont groups. Outside of Bidentalia, it is present in *Dicynodontoides*, *Cistecephalus*, and *Kawingasaurus*, so may represent a synapomorphy of Kistecephalia (postcranial data is deficient for other kistecephalians, however). A supinator process is present in almost all cryptodonts for which postcranial data is available, being present in *Rhachiocephalus*, *Oudenodon*, *Aulacephalodon*, and *Odontocyclops*, but not *Australobarbarus*. Among dicynodontoids, it is absent in all non-kannemeyeriiforms for which humeri are known. Among kannemeyeriiforms with preserved humeri, it is only absent in *Dinodontosaurus*.

174. Morphology of supinator process: 0, low, broadly separated from the shaft; 1, tall and subvertical, with dorsal margin close to base of shaft; 2, discrete, tab-like process occupying restricted portion of anterior face of distal humerus.

In most dicynodonts, the supinator process is a relatively small, low structure proximal to the ectepicondyle but still widely separated from the humeral shaft. In *Pentasaurus*, *Placerias* and *Zambiasaurus* (as well as the unnamed Polish dicynodont [Dzik *et al*. 2008], which is not included in the current analysis) the supinator process is a tall, subvertical ridge extending across nearly the entire edge of the ectepicondyle (Fig. 14A–C). By contrast, in *Eubrachiosaurus*, *Ischigualastia*, and *Stahleckeria*, the supinator process is much more limited in extent and distinct from the ectepicondyle (Fig. 14D; see also Kammerer *et al*. 2013), forming a tab-like structure prominently sticking off of the anterior edge of the humerus (similar to the condition in many early synapsids, e.g. *Dimetrodon*, but unlike any other dicynodonts; Romer 1956). Intriguingly, a somewhat intermediate condition is present in *Angonisaurus*, a taxon that has recently (Angielczyk & Kammerer 2017; Angielczyk *et al*. in press) been recovered immediately outside of the Placeriinae+Stahleckeriinae split. Here, *Angonisaurus* is coded '1', as in placeriines, as its supinator process is subvertical, originates near the base of the humeral shaft, and does not form as much of a distinctly protruding 'tab' as in stahleckeriines. However, unlike in placeriines and more similar to stahleckeriines, the supinator process in

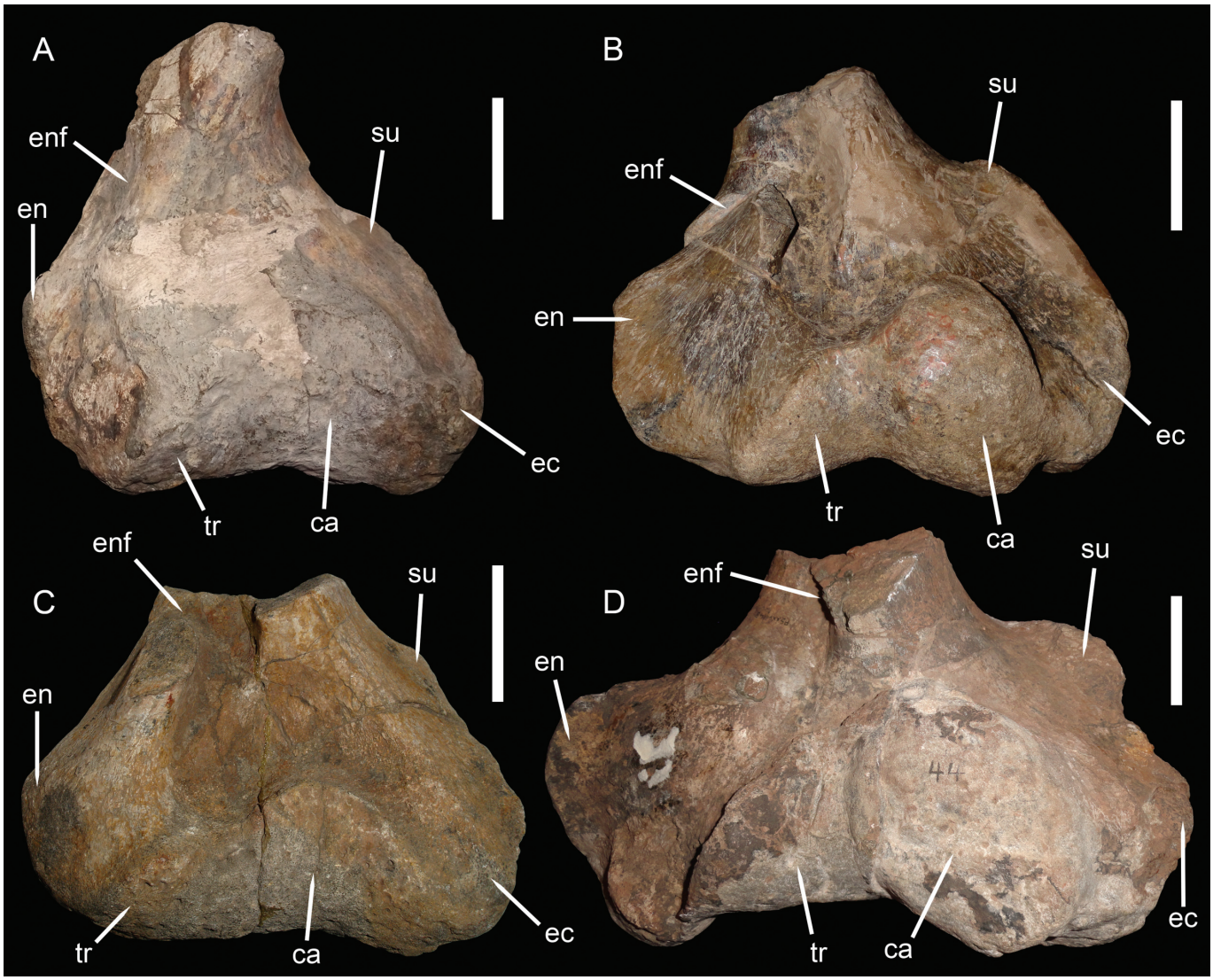

Figure 14. Stahleckeriid distal humeri in ventral view: **A**, *Pentasaurus goggai* (NHMW 1876-VII-B-123); **B**, *Placerias hesternus* (UCMP 25361); **C**, *Zambiasaurus submersus* (NHMUK R9140); **D**, *Stahleckeria potens* (BSPG AS-XXV-148). **A**, **C**, and **D** are left humeri; **B** is a right humerus mirrored for comparative purposes. Note that the radial condyles of **A** and **C** are largely unossified and would have had extensive cartilaginous caps, whereas those of **B** and **D** are well ossified. ca, capitulum; ec, ectepicondyle; en, entepicondyle; enf, entepicondylar foramen; su, supinator process; tr, trochlea. Scale bars equal 5 cm.

Angonisaurus is restricted in extent, and does not extend down to the base of the ectepicondyle. The kistecephalian emydopoids *Dicynodontoides*, *Cistecephalus*, and *Kawingasaurus* have also been coded '1' for this character; although their supinator process is not likely to be homologous with that of placeriines, in these taxa it is also subvertical and originates close to the shaft.

Three most parsimonious trees of length 1143.551 were recovered, differing only in the positions of *Sangusaurus parringtonii* and *Pentasaurus goggai*. *Sangusaurus* is recovered either as the sister-taxon of *Stahleckeria* (in two of the three trees) or the sister-taxon of the clade (*Eubrachiosaurus*+(*Ischigualastia*+*Jachaleria*)). *Pentasaurus* is recovered either as the sister-taxon of *Zambiasaurus* (in two of the three trees) or *Placerias*.

The results of the new analysis (Fig. 21) are generally similar to those of Angielczyk & Kammerer (2017), with a few notable exceptions. Cryptodontia is again recovered as monophyletic, as previously found by Kammerer *et al*. (2011, 2013, 2016), Castanhinha *et al*. (2013), Angielczyk & Cox (2015), Cox & Angielczyk (2015), and Kammerer & Smith (2017), but unlike several recent analyses of anomodont phylogeny (Boos *et al*., 2016; Angielczyk & Kammerer, 2017; Angielczyk *et al*. in press). The composition of the cryptodont subclades largely corresponds to that of Angielczyk & Kammerer (2017), with Geikiidae containing *Idelesaurus* and *Bulbasaurus* in addition to the geikiines and Oudenodontidae containing *Oudenodon*, *Australobarbarus*, and *Tropidostoma*. *Odontocyclops* is recovered as a rhachiocephalid, a novel position for this taxon (in the context of a cladistic analysis; the genus itself was originally based on a species of *Rhachiocephalus*, *R. dubius*), which has otherwise been recovered as an oudenodontid (Kammerer & Smith 2017), a geikiid (Boos *et al*. 2016), or outside of a geikiid+rhachiocephalid clade (e.g. Kammerer *et al*. 2011).

As discussed by Angielczyk & Kammerer (2017), the monophyly (or lack thereof) of Cryptodontia strongly influences the topology of Dicynodontoidea. In analyses where cryptodonts are recovered as monophyletic, the 'elphids' (*Elph*, *Interpresosaurus*, and *Katumbia*) generally fall out as basal dicynodontoids (instead of basal

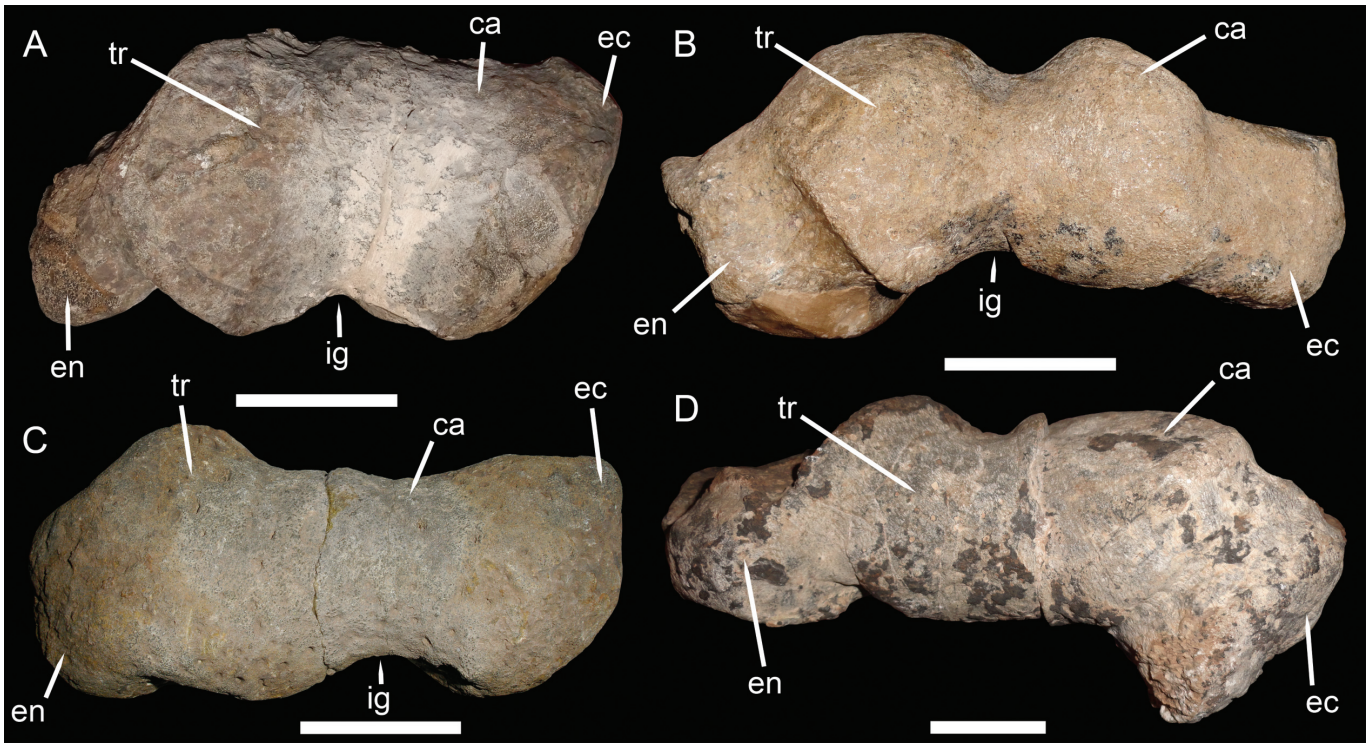

Figure 15. Stahleckeriid humeri in distal view: **A**, *Pentasaurus goggai* (NHMW 1876-VII-B-123); **B**, *Placerias hesternus* (UCMP 25361); **C**, *Zambiasaurus submersus* (NHMUK R9140); **D**, *Stahleckeria potens* (BSPG AS-XXV-148). **A**, **C**, and **D** are left humeri; **B** is a right humerus mirrored for comparative purposes. ca, capitulum; ec, ectepicondyle; en, entepicondyle; ig, intercondylar groove; tr, trochlea. Scale bars equal 5 cm.

bidentalians), and the topology of the remaining Permian dicynodontoids is relatively pectinate. Both of these results are present in the current analysis, at least as regards the Permian dicynodontoids outside of the Lystrosauridae+Kannemeyeriiformes split. Lystrosauridae is expansive in the current analysis, however, and includes the former '*Dicynodon*' (*sensu lato*) species *Euptychognathus bathyrhynchus*, *Gordonia traquairi*, *Jimusaria sinkianensis*, *Sintocephalus alticeps*, and *Syops vanhoepeni* in addition to *Lystrosaurus* itself. With the exception of *Gordonia*, all of these taxa have previously been recovered as lystrosaurids (Kammerer *et al*. 2011), albeit with very low support. Angielczyk & Kammerer (2017) recovered an unusual position for Lystrosauridae (restricted to *Lystrosaurus* in that analysis) at the base of Dicynodontoidea. Lystrosauridae is here recovered as the sister-group of Kannemeyeriiformes, as in most other analyses of anomodont phylogeny (e.g. Kammerer *et al*. 2011, 2013; Castanhinha *et al*. 2013; Cox & Angielczyk 2015; Kammerer & Smith 2017). In general, the relationships among non-kannemeyeriiform dicynodontoids remain extremely volatile, as indicated by the constant flux in dicynodontoid topology between subsequent analyses.

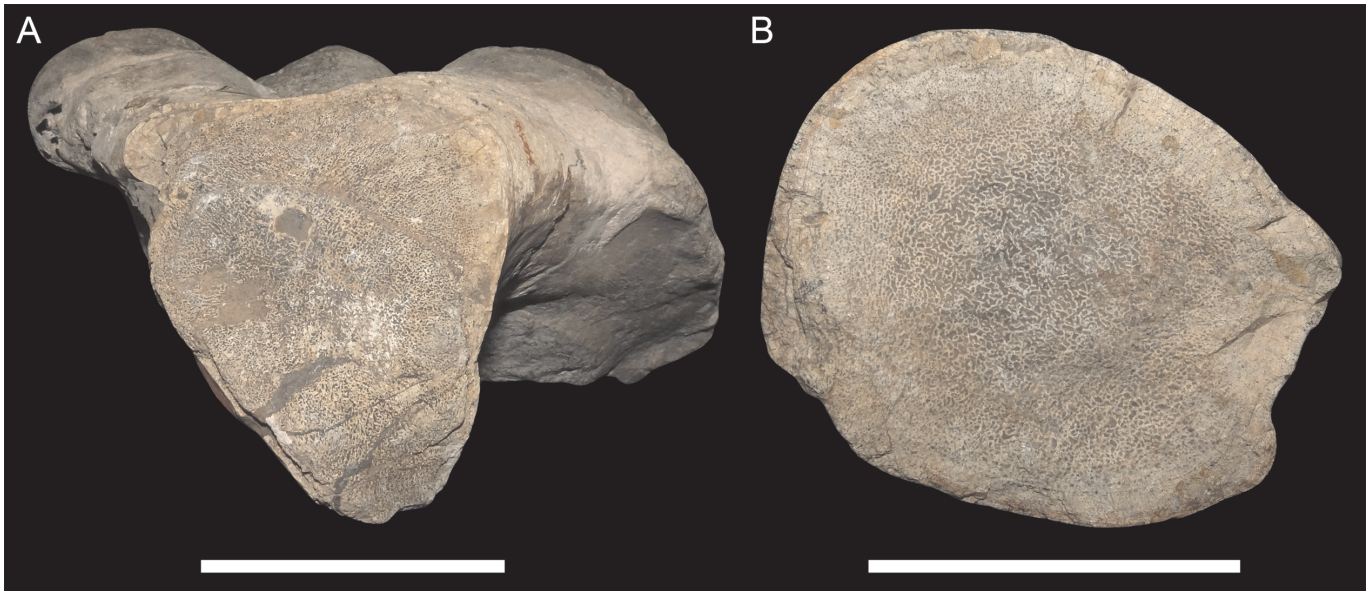

Figure 16. Natural cross-sections through shafts of *Pentasaurus goggai* elements showing internal bone structure: **A**, NHMW 1876-VII-B-123, left humerus in proximal view (downward-pointing process is deltopectoral crest); **B**, NHMW 1876-VII-B-128, right tibia in distal view. Scale bars equal 5 cm.

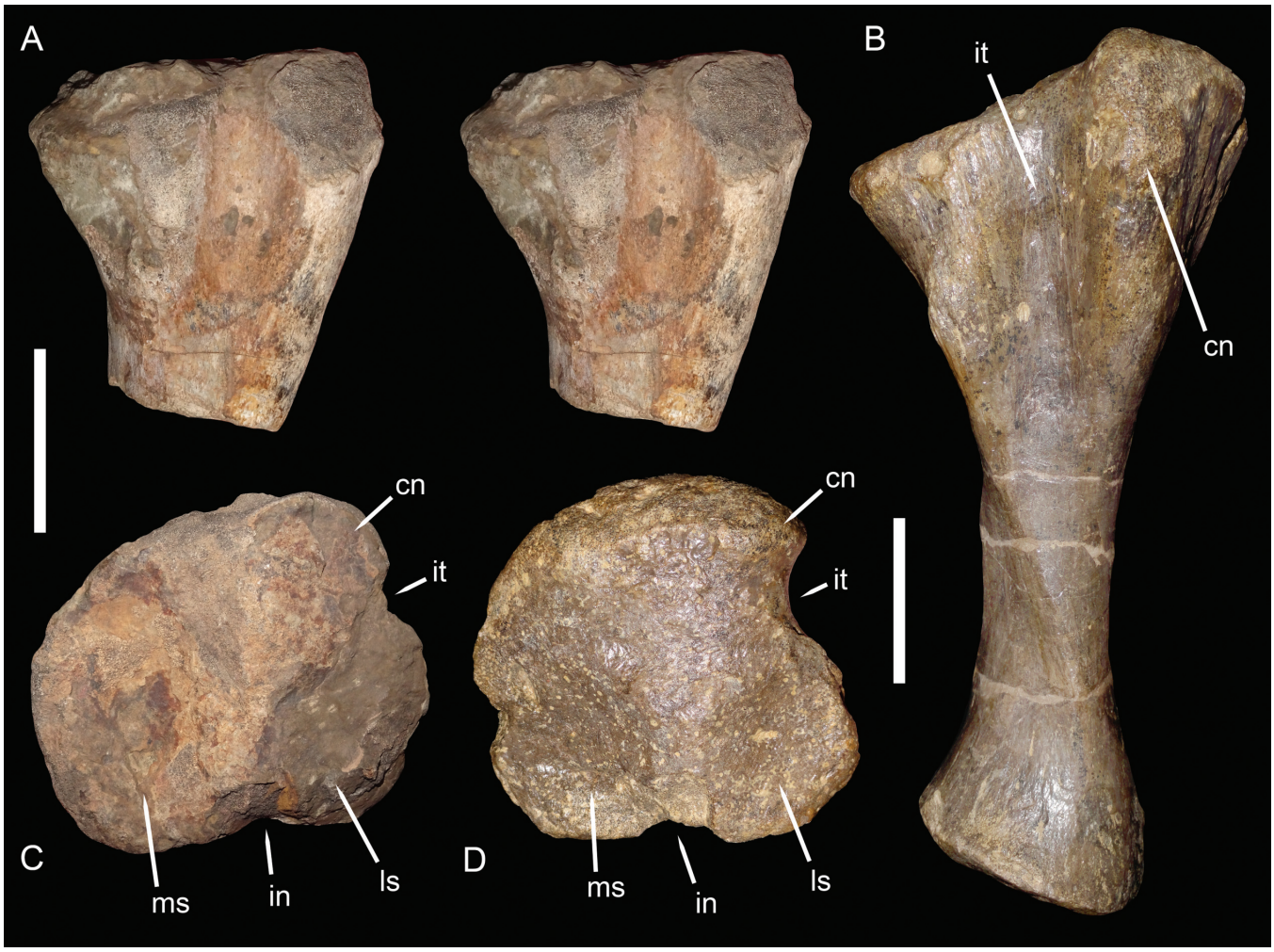

Figure 17. Proximal tibia of *Pentasaurus goggai* (NHMW 1876-VII-B-128) and comparison with *Placerias*. (**A**) Stereopair of right tibia fragment in lateral view and (**C**) element in proximal view. Right tibia of *Placerias hesternus* (UCMP 32447) in (**B**) lateral and (**D**) proximal views. In **C** and **D**, anterior is up. cn, cnemial crest; in, intercondylar notch; it, incisura tibialis; ls, lateral sulcus; ms, medial sulcus. Different views of single specimens to scale with one another. Scale bars equal 5 cm.

Within Kannemeyeriiformes, the results of the current analysis are extremely similar to those of Angielczyk & Kammerer (2017), including the troublesome non-monophyly of Shansiodontidae (traditionally composed of *Shansiodon*, *Rhinodicynodon*, *Tetragonias*, and *Vinceria*, which here form a grade at the base of Kannemeyeriiformes). It is likely that this issue is related to the mosaic of shansiodontid-like and stahleckeriid-like characters present in *Dinodontosaurus*, which is recovered here as more closely related to stahleckeriids than shansiodontids. Further research on *Dinodontosaurus*, which is known from abundant material in the Brazilian Santa Maria Formation (Langer *et al*. 2007) and less abundant but generally better-preserved material in the Argentine Chañares Formation (Mancuso *et al*. 2014), is required to help resolve this issue. The only difference between the current analysis and that of Angielczyk & Kammerer (2017) is the addition of *Pentasaurus*, which destabilizes relationships within Placeriinae. This can probably be attributed to missing data: because of the highly incomplete nature of the known material, *Pentasaurus* could only be coded for a small fraction of the characters in the phylogenetic analysis (22/197).

Figure 18. Long bone fragment (?radius) tentatively referred to *Pentasaurus goggai* (NHMW 1876-VII-B-129). Scale bar equals 5 cm.

DISCUSSION

Identification of the *Pentasaurus* material and its taxonomic distinction

Given the highly fragmentary nature of the material herein described as *Pentasaurus goggai*, further discussion

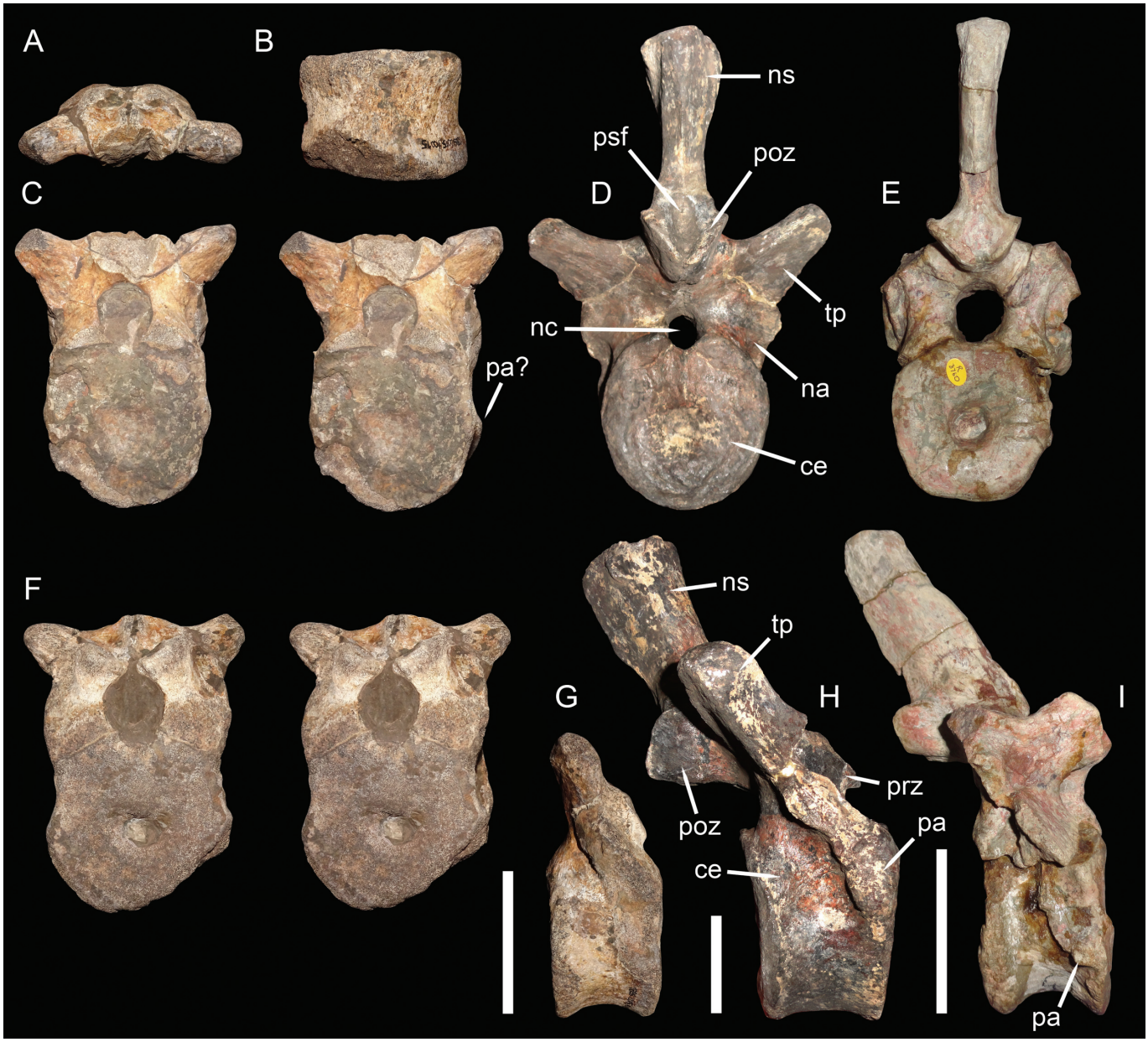

Figure 19. Vertebra of *Pentasaurus goggai* (NHMW 1886-XV-15) and comparisons with other kannemeyeriiforms. Probable cervical vertebra in (**A**) dorsal, (**B**) ventral, and (**G**) right lateral views. Stereopairs of same specimen in (**C**) posterior and (**F**) anterior views. Vertebrae of other kannemeyeriiforms: *Stahleckeria potens* (BSPG AS-XXV-153) anterior dorsal vertebra in (**D**) posterior and (**H**) right lateral views; *Kannemeyeria simocephalus* (NHMUK R3760) cervical vertebra in (**E**) posterior and (**I**) right lateral views. ce, centrum; na, neural arch; nc, neural canal; ns, neural spine; pa, parapophysis; poz, postzygapophysis; prz, prezyapophysis; psf, postspinal fossa; tp, transverse process. Different views of single specimens to scale with one another. Scale bars equal 5 cm.

of its taxonomic unity and distinction from other Triassic dicynodonts is warranted. As there are no repeated elements among the *Pentasaurus* specimens and available evidence indicates that they were found at the same locality, it is tempting to suspect that they represent a single individual. Unfortunately, the limited collection data for these specimens makes it impossible to be certain whether they were found in association. Furthermore, given that Brown's collections from Barnard's Spruit also include definite sauropodomorph and probable 'rauisuchian' specimens, the possibility that other isolated elements from this lot pertain to archosaurs must be carefully considered. None of the elements here referred to *Pentasaurus* resemble 'rauisuchian' bones. The tibia and potential radius fragments (Figs 17, 18) are large and poorly-preserved enough to be mistaken for sauropodomorph elements, but they do not match the histological profile for dinosaurs (see above). Most of the other elements are unmistakably dicynodontian. The fused dentary symphysis forming a toothless 'beak', prominent lateral dentary shelf, and dentary table of NHMW 1876-VII-B-114 allow this specimen to be definitively identified as a dicynodont. The humerus NHMW 1876-VII-B-123 also exhibits an array of features present in therapsids but not sauropodomorphs or 'rauisuchians' (e.g. anteroposteriorly broad distal portion, large, well-defined areas for the capitulum and trochlea, large entepicondylar foramen). Furthermore, both of these elements exhibit features specific to placeriine stahleckeriids among dicynodonts: the combination of a huge

splenial contribution to the jaw symphysis and median symphysial ridge in the jaw fragment and the presence of an elongate, subvertical supinator process on the humerus. The other referred elements all exhibit characteristic dicynodont morphologies, albeit not specific placeriine synapomorphies (see Description above).

The placeriine synapomorphies in the *Pentasaurus* jaw and humerus elements allow ready differentiation from the majority of Triassic dicynodonts. Importantly, mandibular morphology clearly distinguishes NHMW 1876-VII-B-114 from the most common taxon of Karoo kannemeyeriiform, *Kannemeyeria simocephalus* (see Fig. 4). Although survival of the probably Middle Triassic *Kannemeyeria* into the Elliot Formation would be unlikely, the possibility had to be considered, given the possible presence of *Diademodon* (which co-occurs with *Kannemeyeria* in the Burgersdorp Formation) in the lower Elliot (Abdala *et al*. 2007) and general uncertainty as to the Burgersdorp's precise age (Ottone *et al*. 2014). The morphology of the distal humerus NHMW 1876-VII-B-123 permits distinction from stahleckeriines: both the proportions of the humerus and the shape and position of the supinator process differ sharply from that of stahleckeriines (see Fig. 14). The mandibular fragment provides additional characters indicating a non-stahleckeriine identification. A median symphysial ridge, present in NHMW 1876-VII-B-114, is absent in all known stahleckeriines (Kammerer pers. obs.) Additionally, the symphysis in NHMW 1876-VII-B-114 is relatively tall and steeply sloping (Fig. 20E). This is similar to the condition in all other known placeriines (Fig. 20A,B,D), but differs from the more elongate, horizontally-directed symphysis in stahleckeriines (Fig. 20C). Other placeriines also differ from stahleckeriines in that the tip of the 'beak' is shorter by comparison; unfortunately the tip is broken off in NHMW 1876-VII-B-114 so it is unknown whether this feature was shared as well.

Among placeriines, the mandibular morphology of NHMW 1876-VII-B-114 clearly differs from that of *Placerias*, as detailed in the Description above. The same points of distinction largely also apply to *Moghreberia*, although poor preservation of the mandible in that taxon (Fig. 20A) complicates comparisons for certain characters (notably the presence of a sharp edge between the anterior and lateral faces of the symphysis, which is present in in *Placerias*, absent in *Pentasaurus*, and probably present in *Moghreberia*, although this surface is poorly preserved). The most important taxon for comparison in establishing the taxonomic distinctness of the lower Elliot dicynodont material is *Zambiasaurus submersus* from the upper Ntawere Formation of Zambia. As the only other southern African placeriine this taxon is geographically proximate; furthermore, the age of the Ntawere Formation is poorly-constrained and could potentially overlap with the lower Elliot (although it is likely to be older; Angielczyk *et al*. 2014). Regrettably, *Zambiasaurus* is known largely from isolated, juvenile remains (Angielczyk *et al*. 2014), complicating comparisons with the large, presumed subadult-to-adult elements of *Pentasaurus*. With this said, there are a few firm bases for comparison. For one thing, the position and morphology of the lateral dentary shelf is not known to be an ontogenetically variable feature in dicynodonts (Angielczyk *et al*. 2009; Maisch 2009). Although known dentary elements in *Zambiasaurus* are small and poorly preserved (e.g. Fig. 20D), none show any trace of the robust, anteriorly located lateral dentary shelf here considered autapomorphic for *Pentasaurus*. Additionally, one distal humerus fragment of *Zambiasaurus* (NHMUK R9140; Figs 14C, 15C) is substantially larger than the other known *Zambiasaurus* limb elements and is comparable in size to the *Pentasaurus* humerus NHMW 1876-VII-B-123 (Figs 14A, 15A). Although similar in overall shape, in *Pentasaurus* the distal surface of the humerus is substantially more robust and dorsoventrally expanded than in *Zambiasaurus*. Also, the morphology of the entepicondyle differs between these specimens, being relatively truncated in *Pentasaurus*. Although this distinction may be exaggerated by damage to NHMW 1876-VII-B-123, worn bone surface is unlikely to explain all the variation seen between Figures 15A and C. Thus, despite less-than-ideal sets of overlapping material for both taxa, available points of comparison support taxonomic separation between *Pentasaurus* and *Zambiasaurus*.

Identification of the *Pentasauropus* trackmaker

In a series of contributions, Ellenberger (1955, 1970, 1972, 1974) described a diverse ichnofossil assemblage from Stormberg exposures in Lesotho. The majority of Ellenberger's lower Elliot ichnotaxa correspond to reptilian trackmakers (Olsen & Galton 1984), as expected of a Late Triassic tetrapod assemblage, but there are some probable exceptions. One of the most unusual and intriguing of Ellenberger's track morphotypes is a large, pentadactyl print currently known as *Pentasauropus incredibilis* (Ellenberger's ichnotaxonomy, encompassing over 60 ichnogenera and 150 ichnospecies, is generally regarded as highly oversplit, and five ichnospecies are currently considered synonymous with *P. incredibilis*; D'Orazi Porchetti & Nicosia 2007). The zoological attribution of the *Pentasauropus* tracks has long proven problematic. Ellenberger & Ellenberger (1958) initially identified the trackmaker of *Pentasauropus* as either a 'Theromorphe' (=synapsid) or an amphibian. Later, Ellenberger (1970) cited personal correspondence with Donald Baird and A. W. Crompton, who identified the trackmaker as a large dicynodont. Later contributions (e.g. Ellenberger 1972) favored reptilian identification, with a large 'anapsid' reptile or sauropod dinosaur proposed as potential trackmakers. Early revisers of this ichnofossil assemblage were similarly circumspect: Haubold (1974) considered the trackmaker of *Pentasauropus* to be either a sauropod or an anomodont. Subsequent research has generally favoured a dicynodont identification for the *Pentasauropus* trackmaker, however (e.g. Demathieu & Haubold 1974; Hopson 1984; Olsen & Galton 1984; Anderson *et al*. 1998; Lockley & Meyer 2000; Gaston *et al*. 2003; Lockley *et al*. 2006). Olsen & Galton (1984, p. 97) called these tracks 'unmistakable' despite their poor preservation, and flatly stated that dicynodonts represent the 'only early Meso-

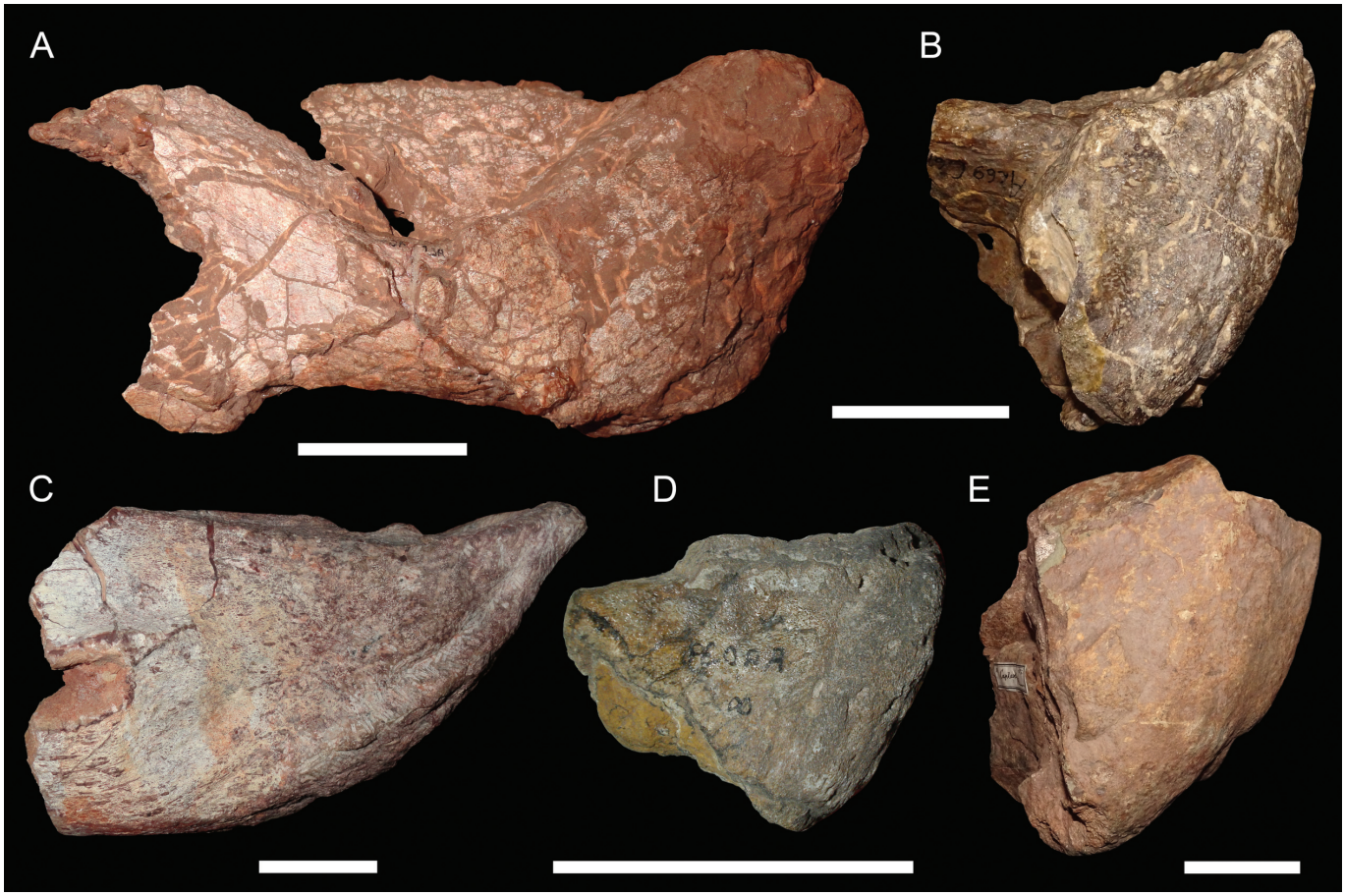

Figure 20. Anterior portions of stahleckeriid mandibles in lateral view: **A**, *Moghreberia nmachouensis* (MNHN.ALM.167); **B**, *Placerias hesternus* (GPIT/RE/9578); **C**, *Stahleckeria potens* (AMNH FARB 7804); **D**, *Zambiasaurus submersus* (NHMUK R9039); **E**, *Pentasaurus goggai* (NHMW 1876-VII-B-114). Note relatively tall, steep symphyses of placeriines (**A**, **B**, **D**, **E**) compared to the more elongate, gently curved symphysis of a typical stahleckeriine (**C**). Specimens in **B** and **E** in right lateral view; **A**, **C**, and **D** in left lateral view but mirrored for comparative purposes. Scale bars equal 5 cm.

zoic… group with feet both large enough and with toes short enough to have made *Pentasauropus*-type tracks'. Despite majority support for the '*Pentasauropus* as dicynodont track' hypothesis, in recent years there have been a few dissenting opinions. Knoll (2004) deemed the dicynodont affinities of *Pentasauropus* unconvincing and argued that it could also be sauropodan. Hunt & Lucas (2007) stated that while only dicynodonts represent a good match for the *Pentasauropus* prints morphologically, they doubted this attribution based on the absence of skeletal evidence for dicynodonts of equivalent age to the tracks (speaking specifically of North American records [Lockley & Hunt 1995], but applicable to the southern African record as well).

The most recent revisionary work on the Lesotho trackways (D'Orazi Porchetti & Nicosia 2007) has convincingly demonstrated that the *Pentasauropus* tracks do not match sauropodomorph autopodia. Many of the tracks from the Stormberg of Lesotho (e.g. *Tetrasauropus* and *Pseudotetrasauropus*) do show indications of a sauropodomorph trackmaker and differ dramatically from those of *Pentasauropus*. As regards Hunt & Lucas' (2007) issue that dicynodonts must have gone extinct prior to the *Pentasauropus* tracks being laid down, several lines of evidence now address this problem. Firstly, although precise chronostratigraphic dating remains elusive for many Triassic vertebrate assemblages worldwide, there is increasingly good evidence that a number of stahleckeriid dicynodont-bearing deposits are actually Norian in age (Irmis *et al*. 2011; Kent *et al*. 2014; note also that Dzik *et al*. [2008] even proposed a Rhaetian age for Polish stahleckeriid remains). So arguments based on a prior understanding of dicynodonts having gone extinct at the end of the Carnian (e.g. Benton 2006) are no longer tenable. Secondly, concerning the southern African record in particular, it is true that historically there has been no skeletal evidence for dicynodonts surviving in the Karoo Basin above the (probably) Middle Triassic Burgersdorp Formation. As the Elliot Formation is reasonably well-sampled (Smith *et al*. 2012), this seemed to be good evidence that dicynodonts truly were absent there in the Late Triassic. However, raw sampling is often not equivalent to subsequent worker research effort, and researchers working in collections frequently overlook specimens that do not fit the search image for their taxon of interest. This can make the absence of certain taxa in even well-sampled deposits something of a 'self-fulfilling prophecy': if researchers do not expect to find a given taxon, they may not look for it, and specialists on that taxon will eschew collections that (supposedly) contain no representatives of it. As clear evidence of this, the specimens described herein were housed in one of the largest and most frequently visited palaeontological collections in Europe for over 140 years without any recognition of their taxonomic identification and importance. It is possible that additional dicynodont elements remain unrecognized in other lower Elliot collections.

Given that the *Pentasauropus incredibilis* tracks from the lower Elliot Formation morphologically match a dicynodont trackmaker, and that dicynodonts were indeed present in this formation (based on the newly-described fossils herein), can it be demonstrated that the

Figure 21. Results of the phylogenetic analysis: subtree showing the relationships of Bidentalia. Non-bidentalian anomodont relationships are identical to those of Angielczyk & Kammerer (2017). Numbers at nodes represent symmetric resampling values.

taxon here named *Pentasaurus* was actually the trackmaker of *Pentasauropus*? On a strict morphology basis, the answer is no. No manus or pes elements are preserved among the known material of *Pentasaurus*, so direct comparisons are not possible. Furthermore, known kannemeyeriiform manual and pedal materials are generally homomorphic, suggesting morphological conservatism of these elements across the clade. Observed variation in manus morphology among kannemeyeriiforms has mostly been limited to minor differences in ungual shape (Cox 1965; Lucas 2002); it is uncertain to what degree, if any, this would be reflected

in *Pentasauropus*-type trackways. As such, even if *Pentasaurus* autopodia were known, unique correspondence with the *Pentasauropus incredibilis* tracks would be unlikely. Indeed, tracks referred to *Pentasauropus* have also been reported from North (Lockley & Hunt 1995; Gaston *et al*. 2003) and South America (Domnanovich *et al*. 2008); these tracks likely represent various local kannemeyeriiform taxa (*Placerias*, *Ischigualastia*, etc.) However, while a morphological correlation between *Pentasaurus goggai* and *Pentasauropus incredibilis* is not currently possible (and may never be), a strong circumstantial case can be made for *Pentasaurus* as the trackmaker of lower Elliot *Pentasauropus* prints. Although dicynodonts are now thought to have survived into the Norian, they were rare and species-poor at this time. No Norian basins are known to produce more than a single dicynodont species. Kammerer *et al*. (2013) recently resurrected *Eubrachiosaurus browni* from the Popo Agie Formation of Wyoming as a valid taxon, bringing the number of Triassic North American dicynodont species to two (the other being the well-known *Placerias hesternus*). However, no localities are known to produce both *Eubrachiosaurus* and *Placerias*, and increasing evidence indicates that the tetrapod fauna of the Popo Agie Formation is not coeval with the *Placerias*-bearing beds of the Chinle Formation, instead representing a substantially older (potentially Carnian) assemblage (Hartman *et al*. 2015). In South America, one endemic species each is known from the Los Colorados Formation of Argentina (*Jachaleria colorata*) and the Caturrita Formation of Brazil (*Jachaleria candelariensis*) (Arcucci *et al*. 2004; Müller *et al*. 2015). It is highly unlikely that the lower Elliot Formation would have diverged from this pattern, particularly given the rarity of dicynodont fossils in this formation relative to other Norian deposits (while additional *Pentasaurus* remains may well be lying unrecognized in South African collections, its record is clearly poorer than the likes of *Placerias* and *Jachaleria*, which are known from multiple skulls). In conclusion, there is no good reason to suspect any dicynodont taxa other than *Pentasaurus goggai* were present in the lower Elliot Formation, making it the only probable trackmaker of regional *Pentasauropus* trackways.

Biogeographic and faunal implications

The recognition of a placeriine dicynodont in the lower Elliot Formation conflicts with several prevailing ideas on Late Triassic dicynodont survival, namely their supposed absence in the Karoo Basin in strata above the Burgersdorp Formation (Rubidge 1995), the supposed disjunct between Triassic faunas containing dicynodonts *vs* sauropodomorph dinosaurs as the largest-bodied herbivores (Benton 1994), and the recognition of Placeriinae as a predominantly Northern Hemisphere clade (Kammerer *et al*. 2013, in press).

The lack of co-occurrence between large-bodied kannemeyeriiform dicynodonts and the earliest large dinosaurian herbivores (sauropodomorphs) has frequently been discussed by Triassic researchers in the context of synapsid/archosaur turnover patterns (Bakker 1977; Benton 1983, 2006; Charig 1984; Zawiskie 1986; Brusatte *et al*. 2008; Benton *et al*. 2014). The prevailing idea in the late 20th and early 21st centuries was that dicynodonts went extinct at the end of the Carnian, whereas the first large-bodied sauropodomorphs did not appear until the Norian (Benton 1994). Thus, direct ecological interaction between dicynodonts and sauropodomorphs was thought not to have occurred, regardless of whether the researchers in question supported environmental change (e.g. Benton 1983) or clade-level competition with archosaurs (e.g. Charig 1984) as the primary driver of Triassic synapsid decline. As discussed in the preceding section, new radioisotopic and magnetostratigraphic dates for Late Triassic vertebrate assemblages now indicate that dicynodonts survived into the Norian (Irmis *et al*. 2011; Kent *et al*. 2014). However, even with this extension of the clade's range, there has until now been no evidence of direct co-occurrence between dicynodonts and large-bodied sauropodomorphs. The youngest dicynodont remains from South America (and the youngest securely dated dicynodonts worldwide) are those of *Jachaleria colorata* from the Norian Los Colorados Formation of Argentina (Kent *et al*. 2014). The Los Colorados Formation also contains a diverse sauropodomorph assemblage including the taxa *Coloradisaurus*, *Riojasaurus*, and the enormous (~9 m) *Lessemsaurus* (Pol & Powell 2007). However, these taxa are known only from the upper part of the formation, whereas *Jachaleria* is known only from the base of the formation (Arcucci *et al*. 2004). Disarticulated archosaur specimens that may represent sauropodomorphs have been recovered from the basal Los Colorados, in the same levels as *Jachaleria*, but they are currently undescribed (Martínez *et al*. 1998). The preliminarily-described kannemeyeriiform from the Lisowice claypit in Poland was originally stated to be Rhaetian (Dzik *et al*. 2008), but this site may also be Norian (Niedźwiedzki & Sulej 2008), and regardless of age has not produced any sauropodomorph material. Thus, the presence of *Pentasaurus* and *Eucnemesaurus* in the material from Barnard's Spruit potentially represents the first co-occurrence of a dicynodont and large sauropodomorph in the Triassic.

Kammerer *et al*. (2013, in press) commented on the global distribution of stahleckeriids, noting an apparent geographic disjunct between its two subclades, with stahleckeriine fossils mostly found in the Southern Hemisphere and placeriine fossils mostly in the Northern. They recognized exceptions to this pattern, however, with the stahleckeriine *Eubrachiosaurus browni* known from the Popo Agie Formation of the western United States (Wyoming) and the placeriine *Zambiasaurus submersus* known from the Ntawere Formation of Zambia. *Pentasaurus goggai* represents an additional exception to this supposed pattern, joining *Zambiasaurus* among the ranks of southern Gondwanan placeriines. Furthermore, it refutes the hypothesis that while placeriines may have originated in Gondwana in the Middle Triassic, their Late Triassic radiation was confined to the Northern Hemisphere. The presence of *Pentasaurus* in the lower Elliot demonstrates that this clade was present across Pangaea even in the Late Triassic.

Environmental restriction offers a common explanation for the conflicts between the three aforementioned prevailing ideas on Triassic dicynodont distribution and the presence of *Pentasaurus* in the lower Elliot Formation. Late Triassic dicynodont fossils show a distinctly 'patchy' distribution, best illustrated by *Placerias hesternus*. This taxon is generally one of the rarest components of North American Triassic assemblages, but in a few exceptional localities represents the dominant taxon (most notably the *Placerias* Quarry near St. Johns, Arizona; Lucas & Heckert 2002). Massive accumulations like the *Placerias* Quarry indicate that *P. hesternus* was not just a rare, solitary animal, but more likely was an ecologically-restricted taxon that did not prefer or could not tolerate the seasonally arid environments preserving most Chinle Formation tetrapod fossils. Notably, the Blue Mesa Member of the Chinle Formation, which has produced the majority of *Placerias* fossils, seems to preserve one of the wettest sections of the Chinle (Martz & Parker 2010). Additionally, although only preliminarily studied, *Placerias* seems to be more abundant in the more humid basins of the Newark Supergroup in eastern North America (Baird & Patterson 1968; Kammerer *et al*. 2013). This would concord with broader-scale studies indicating the restriction of synapsids to humid belts in the Late Triassic (Whiteside *et al*. 2011). Thus, synapsids could still have been extremely abundant in 'patches' of the appropriate habitat in the Late Triassic, but if that specific habitat is not preserved, they would appear to be absent in the regional record. Although less arid than the upper Elliot (with perennial river systems; Bordy & Eriksson 2015), the lower Elliot still represents a relatively arid environment compared to earlier Triassic dicynodont-bearing deposits (e.g. Smith & Swart 2002), and it is likely that the majority of fossiliferous localities in the lower Elliot simply do not preserve the sort of wet habitat frequented by Late Triassic dicynodonts. As such, the co-occurrence of a kannemeyeriiform and large sauropodomorph like *Pentasaurus* and *Eucnemesaurus* may represent an unusual circumstance, and these taxa may well have rarely encountered each other when alive, because of their preferences for different kinds of vegetation (see Benton 1983; Crompton & Attridge 1986).

The apparent geographic disjunct between placeriine and stahleckeriine stahleckeriids in the Carnian-Norian is more difficult to explain, but is also probably attributable to environmental specializations of the respective clades. Work on functional variation in the dicynodont feeding apparatus has generally focused on very broad trends, such as the differences between Permian and Triassic dicynodonts (e.g. Crompton & Hotton 1967). Unfortunately, little attention has been given to the functional implications of differences in morphology within Kannemeyeriiformes. Surkov & Benton (2008) attempted to reconstruct feeding height in dicynodonts and preferred plane of head movement based on occipital morphology and included a number of Triassic taxa in their analysis. They measured differences in the relative height and width of the occiput, which they took to reflect differences in relative efficiency of the lateral and dorsal portions of the neck musculature. Dicynodonts with heads low to the ground would be expected to use more lateral movements, whereas dicynodonts feeding high would require greater development of the dorsal neck musculature to hold the head up. Under this scheme, Surkov & Benton (2008) reconstructed *Placerias* as a high-level feeder and *Stahleckeria* as a low-level feeder. While these results suggest that general cranial conservatism belies sharp differences in feeding behavior between kannemeyeriiform taxa, occipital dimensions are only part of the story: other trophically relevant morphological features of these taxa still await detailed comparisons. As shown by Angielczyk *et al*. (in press), position and angulation of jaw muscles would also have strongly influenced dicynodont feeding style, but rigorous reconstructions are currently available for only a small handful of taxa. Mandibular morphology is also understudied, and the functional implications of differences in dicynodont jaw shape are poorly known. The narrower, taller symphyses of placeriines (Figs 5, 20) do suggest that they were concentrating greater bite force on the 'beak' tip than stahleckeriines, possibly reflecting differences in preferred diet (as suggested by Cox [1965] for kannemeyeriids *vs* stahleckeriids). Observed distribution of the two stahleckeriid subclades, then, may just be reflective of local abundance of preferred vegetation, with apparent rarity in one hemisphere or another representing sampling artefact. However, the situation is complex: despite the similarity of their mandibular morphology and inferred myology to *Stahleckeria*, other stahleckeriines (*Ischigualastia* and *Jachaleria*) were reconstructed by Surkov & Benton (2008) as high-feeders, with similar occipital values to *Placerias*. So it is probably premature to propose general, clade-specific feeding specializations for placeriines *vs* stahleckeriines that explain their distribution. Extensive additional research will be required to incorporate these various sources of data into a holistic view of kannemeyeriiform feeding, and as *Pentasaurus* indicates, there remains much left to learn about the palaeobiology of the latest-surviving dicynodonts.

ABBREVIATIONS

Institutional

AMNH FARB	American Museum of Natural History, Fossil Amphibian, Reptile, and Bird Collection, New York, U.S.A.
BP	Evolutionary Studies Institute (ESI), University of the Witwatersrand, Johannesburg, South Africa
BSPG	Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany
ELM	East London Museum, East London, South Africa
FMNH	Field Museum of Natural History, Chicago, U.S.A.
GPIT	Paläontologische Sammlung, Eberhard Karls Universität Tübingen, Tübingen, Germany
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China
MACN	Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina
MCN	Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil
MNA	Museum of Northern Arizona, Flagstaff, U.S.A.
NHMUK	The Natural History Museum, London, U.K.

NHMW	Naturhistorisches Museum Wien, Vienna, Austria
NMT	National Museum of Tanzania, Dar es Salaam, Tanzania
PVL	Fundación Miguel Lillo, Sección de Paleovertebrados, Tucumán, Argentina
SAM	Iziko South African Museums, Cape Town, South Africa
UCMP	University of California Museum of Paleontology, Berkeley, U.S.A.
UFRGS	Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil
UMZC	University Museum of Zoology, Cambridge, U.K.
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.

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